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STUDIES IN THE BORAGINACEAE, XI

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1. THE SPECIES OF *TOURNEFORTIA* AND *MESSERSCHMIDIA* IN THE OLD WORLD

THE SPECIES treated here have, in the past, all been referred to the genus *Tournefortia*. I am, however, suggesting that certain of them be segregated to form the redefined genus *Messerschmidia*. During the work on this paper I have been privileged to examine almost all the type-specimens concerned. This has permitted me to place definitely a large number of poorly understood old species that have troubled workers in the past. The work has been undertaken as part of a projected study of the Boraginaceae-Heliotropioideae. It is the first attempt to treat all the Old World species of *Tournefortia* since the presentation by DeCandolle in the ninth volume of the *Prodromus* in 1845.

Tournefortia Linnaeus, Sp. Pl. 140 (1753) and Gen. Pl. ed. 5, 68 (1754).

The species of *Tournefortia* found in the Old World all belong to the following:

Section **EUTOURNEFORTIA** Johnston, Contr. Gray Herb. 92: 66 (1930). — type-species, *T. hirsutissima* L. *Tournefortia* — *Pittoniae* Humboldt, Bonpland & Kunth, Nov. Gen. et Sp. 3: 80 (1818). — type-

species, *T. hirsutissima* L. *Tournefortia* sect. *Pittonia* Don, Gen. Syst. 4: 366 (1837).—type-species, *T. hirsutissima* L. *Pittonia* Plumier ex Adanson, Fam. Pl. 2: 177 (1763).—type-species, *T. hirsutissima* L. *Oskampia* Rafinesque, Sylva Tellur. 123 (1838).—type-species, *O. scandens* Raf. & *O. hirsuta* Raf. *Tournefortia* sect. *Tetrandra* DeCandolle, Prodr. 9: 527 (1845).—type-species, *T. tetrandra* Blume. *Tetrandra* (DC.) Miquel, Fl. Nederl. Ind. 2: 928 (1858).—type-species, *Tournefortia tetrandra* Blume.

The species of *Eutournefortia* found in the Old World are remarkable for their parallelism of variation. Most of them have corollas with the tube either long or short, herbage with the pubescence present or absent, as well as leaf-blades that are broad or elongate. The combinations of these variations produce forms very diverse in gross appearance so that it is not at all surprising that botanists have been impressed by them and misled into giving specific names to many of them. A consideration of all the Old World *Eutournefortiae* and observation of the recurrent pattern of variation among them, however, lead one to a proper estimate of the surprisingly diverse phases which they present. Likewise, a consideration of the facts of distribution leads to a similar end. When the variations mentioned are given recognition it is found that the resulting numerous ill defined "species" grow together over most of a common area of dispersal. When the variations mentioned are discounted, species may be defined that have a credible geographic range—a range that is distinct from that of the closely related species and one quite similar and familiar among species of other genera within the region. I am accordingly of the opinion that the variations noted deserve at best no more than mere formal recognition. Since, however, I do not believe that obscure tropical plants should be burdened with numerous subspecific names until some evident use for them arises, I have refrained from any attempt at formally naming the reoccurring combinations of the paralleling intraspecific variations described.

KEY TO THE SPECIES

- Ripened fruit breaking up into four equal single-seeded nutlets,
these prominently ribbed on their inner surface1. *T. sarmentosa*.
Ripened fruit breaking up into two carpels which are each composed of two seminiferous cells and an intervening empty one.
Flowers 4-merous2. *T. tetrandra*.
Flowers 5-merous.
Continental plants from southern Asia (including the Andaman Islands).

Calyx-lobes 3-4 mm. long at anthesis, usually subulate; leaves drying more or less golden-brown beneath; Sikkim.3. *T. Hookeri*.

Calyx-lobes 1-2 mm. long at anthesis, linear or lanceolate.

Flowers with evident pedicels 1-2 mm. long; Madras (cf. no. 5)4. *T. Heyneana*.

Flowers sessile or subsessile.

Leaves abruptly long acuminate, blade more or less oval; flowers and fruit usually shortly pedicellate; Southern Burma and the Andamans....5. *T. ovata*.

Leaves short-acuminate and usually not abruptly so; blades oblong to lanceolate; flowers and fruit sessile6. *T. montana*.

Insular plants.

Western Pacific Ocean.

Leaves opposite, flowers sessile; Philippines.....7. *T. luzonica*.

Leaves alternate; flowers short-pedicellate; Australia and Papua8. *T. Muellieri*.

Western Indian Ocean.

Leaves obtuse or rounded at base, 4-11 cm. long...9. *T. puberula*.

Leaves acute at base, 10-20 cm. long.

Stems with minute short closely appressed brownish or golden hairs or quite glabrous; calyx very sparsely strigose, the lobes cuneate, more or less erect; Reunion10. *T. acuminata*.

Stems with evident abundant loosely appressed hairs (usually more or less velvety); calyx usually distinctly hairy with the lobes more or less spreading.

Sepals ovate; Reunion11. *T. arborescens*.

Sepals lanceolate; Mauritius12. *T. Bojeri*.

1. ***Tournefortia sarmentosa*** Lamarck, Tab. Encyc. 1: 416 (1791); Poiret, Encyc. 5: 357 (1804). *Tournefortia orientalis* R. Brown, Prod. 497 (1810); Banks & Solander, Bot. Cook's Voy. 2: 64, tab. 210 (1901). *Tournefortia tetrandra* var. *hirsuta* Blume, Bijdrag. Fl. Nederl. Ind. 845 (1826). *Tournefortia sarmentosa* var. *hirsuta* Blume ex Miquel, Fl. Ind. Batav. 2: 927 (1858), lapsus. *Tournefortia hirsuta* Reinwardt ex Boerlage, Hand. Fl. Nederl. Ind. 2²: 487 (1899). *Tournefortia Urvilleana* Chamisso, Linnaea 4: 465 (1829). *Tournefortia frangulaefolia* Zippel ex Spanoghe, Linnaea 15: 334 (1841 ?), in synon. *Tournefortia Horsfieldii* Miquel, Fl. Ind. Batav. 2: 927 (1858). *Tournefortia acclinis* F. v. Mueller, Frag. 4: 95 (1864). *Tournefortia macrophylla* K. Schumann & Lauterbach, Fl. Deutsch. Schutzgeb. Südsee 520 (1901). *Tournefortia sarmentosa* var. *magnifolia* Domin, Bibl. Bot. 22(Heft 89⁴): 1097 (1928). *Tournefortia glabriifolia* Domin, Bibl. Bot. 22(Heft 89⁴): 1098 (1928).

Java to New Guinea, southward into northern Queensland and northward through the Celebes, Moluccas and Philippines to Formosa.

A variable plant but readily recognized, even in its most diverse forms, by its characteristic fruit. At maturity this breaks up into four equal single-seeded nutlets. All the other Old World *Tournefortiae* have fruits with two 2-seeded carpels. *Tournefortia sarmentosa* has been repeatedly confused with continental species and has been the victim of numerous unsuccessful attempts at segregation. In *T. sarmentosa* the corollas may be either long or short, the herbage either glabrous or pubescent and the leaf-blades either small or large. These characters in various combinations have produced a host of forms that are superficially very diverse in appearance. These forms, however, agree in fundamental fruiting structures. None of them shows any evident geographical correlation. Grouped together to constitute *T. sarmentosa*, as here accepted, they appear as mere phases in a species which has a range that is natural and is of a type quite familiar to any student of the Malaysian flora.

The type of *T. sarmentosa*, in the Lamarck Herbarium at Paris, is labeled "colitur in horto regio insulae Franciae" and "de M. Sonnerat." It is a good specimen showing leaves and flowers but no fruit. The corolla has a tube ca. 2 mm. long and a limb ca. 2.5 mm. in diameter. The calyx is 1.5 mm. long and has broad hairy lobes. The inflorescence is velvety with a dense short but somewhat shaggy, tan-colored indument. The stems and under surface of the leaves have abundant gray hairs. The upper surface of the leaves are green and only sparsely strigose. The petiole is ca. 1 cm. long. The blade is rounded at the base, acute at the apex, and is 7.5–10 cm. long and 2.8–4 cm. broad. The plant is evidently the small-flowered hairy form of the common *Tournefortia* of the East Indian islands. It is certainly not a native of the Mascarenes! Gagnepain, Not. Syst. 3: 32–33 (1914), has discussed this species. His notes, except those referring to collections by Spire, Thorel, and Watt, all refer to the species as I have taken it. The excluded collections are from the Asiatic continent. The species is restricted to the islands and is not to be expected from the mainland.

The type of *T. orientalis*, at the British Museum, is labeled as collected in 1770 by Banks and Solander at Endeavor Bay in northern Queensland. It is a glabrous plant with ovate to oblong leaves, 7–9 cm. long and 3.5–6.5 cm. broad. The corollas are large with a tube ca. 8–9 mm. long and a limb 3–4 mm. broad.

The type of *T. Urvilleana* was collected by Chamisso in Luzon. It has corollas 8 mm. long and a limb 3 mm. broad. The leaves are slightly less pubescent but otherwise are as in the type of *T. sarmentosa*.

Blume's *T. tetrandra* var. *hirsuta* is given as from the Moluccas and described as follows: "ramis foliis pedunculisque hirsutissimis." At Leiden there is a specimen labeled: "Variet.; Tournefortia hirsuta; Manado; *T. tetrandra* Bl. Variet." The first and the last items are in Blume's script. The specimen is a form with elongate corollas and with more or less hairy leaves suggesting those of *T. Horsfieldii*. Manado is near the northern tip of the Celebes. Another specimen at Leiden has the following label: "1531 Tournefortia hirsuta R.; Habitat in insula Celebes ad viam inter Kema et Manado; Oct. 1821." This is associated with a printed label reading "Herbarium Reinwardtianum; in Acad. Lugduno-Batavia." This second specimen is similar to that first mentioned and both are probably collections made by Reinwardt. They are, I believe, the types of *T. tetrandra* var. *hirsuta* and *T. hirsuta*.

The name *T. frangulaefolia* Zippel has appeared only in synonymy. At Leiden this name appears on two sheets having a printed label bearing: "Herb. Lugd. Batav.; Timor" and one in script reading: "1/6 Tournefortia frangulaefolia; Zp."

Miquel based his *T. Horsfieldii* upon material cited: "Java, in Patjitan, Kelak (Horsf.)." I have examined specimens from Horsfield's personal herbarium at the British Museum and those from the set he made for the East India Company (now kept as a unit) at Kew. He made two collections referable to *T. sarmentosa*, 1: Pajittan (Kalak) Horsfield (borage 6) no. 275; and 2: Blambangan, Horsfield (borage 7) no. 309. The former is evidently the type collection of *T. Horsfieldii*. It is a plant with very large leaves that are grayish velvety beneath. The blade becomes 10–14 cm. long and 7–9 cm. broad. The corolla-tube is 7–8 mm. long and the limb is 3–4 mm. broad.

Tournefortia acclinis is based upon material from Queensland collected by Bowman at Broad Sound and Amity Creek, and by Dallachy at Edgcombe Bay. A study of the original description and of a duplicate of Dallachy's material at Kew shows this species to have moderately sized leaves (5–10 cm. long and 3.5–6 cm. broad), a coarse appressed pubescence, a corolla with a tube 3–5 mm. long, and a corolla-limb 3–4 mm. broad. It is very similar to *T. Horsfieldii*, except in leaf-size.

The type of *T. macrophylla* was collected by Lauterbach (no. 2003) at Erima in eastern New Guinea. It is in fruit. The leaves are similar in size and shape to those of typical *T. Horsfieldii*. In fact the plant differs from the type of that species only in the practical absence of pubescence. The leaves have only a few weak scattered inconspicuous hairs along the nerves.

Domin's *T. sarmentosa* var. *magnifolia* from northern Queensland

(*Dietrich* 724), to judge from description, seems to be merely a form of *T. sarmentosa* with very large (12–15 cm. long, 6–6.5 cm. broad) hairy leaves, and small corollas (corollae tubo breviores). His *T. glabrifolia* is another large-leaved (10–13 cm. long and 5–5.5 cm. broad) plant. The leaves are glabrous. The corolla-tube is ca. 3–4 mm. long and the limb is ca. 2 mm. broad. The plant comes from Harvey's Creek in northeastern Queensland. It appears to differ from the type of *T. orientalis* only in its larger leaves and smaller corollas.

2. *Tournefortia tetrandra* Blume, *Bijdrag. Fl. Nederl. Ind.* 845 (1826). *Tournefortia tetragona* Blume ex Steudal, *Nomencl. ed. 2*, 2: 694 (1841). (?) *Heliotropium scandens* Norona, *Verh. Bat. Genootsch.* 5: 78 (1827); Hasskarl, *Cat. Hort. Bogor.* 137 (1844), nomen. *Tournefortia tetrandra* var. *glabra* Hasskarl, *Flora* 25²: Beibl., p. 27 (1842); Hasskarl, *Cat. Hort. Bogor.* 137 (1844); Hasskarl, *Pl. Javan. Rariores* 492 (1848). *Tournefortia glabra* (Hassk.) Zollinger & Moritzi ex Zollinger, *Natuur- en Geneeskundig Archief v. Nederl. Ind.* 2: 5 (1845). *Tetrandra glabra* (Hassk.) Miquel, *Fl. Nederl. Ind.* 2: 929 (1858). *Tournefortia tetrandra* var. *longiflora* Hasskarl, *Cat. Hort. Bogor.* 137 (1844), nomen; Hasskarl, *Pl. Javan. Rariores* 492 (1848). *Tournefortia Wallichii* DeCandolle, *Prodr.* 9: 527 (1845); Ridley, *Fl. Malay Penin.* 2: 441, fig. 115 (1923). *Tetrandra Wallichii* (DC.) Miquel, *Fl. Nederl. Ind.* 2: 928 (1858). *Tetrandra Zollingeri* Miquel, *Fl. Nederl. Ind.* 2: 928 (1858).

Nicobar Islands, Malay Peninsula, Sumatra, Java, Borneo and Celebes.

This is apparently the most common and best known of the Javan species of *Eutournefortia*. The Javan plant has received the following basic names, *Tournefortia tetrandra* Blume, *Tournefortia tetrandra* var. *glabra* Hassk., *Tournefortia tetrandra* var. *longiflora* Hassk., and *Tetrandra Zollingeri* Miquel. The differences between these named forms are minor and variable ones of corolla-size and of distribution of pubescence on the foliage. This variable plant of Java I am quite unable to distinguish from *Tournefortia Wallichii* DC., a species based upon material from Singapore and Penang. I have accordingly accepted *Tournefortia tetrandra* as ranging from the Nicobar Islands eastward to Java and the Celebes. The leaves of this species are ovate-acuminate or lance-ovate and are glabrous or sparsely strigose. The fruit is usually subglobose and 4–6 mm. in diameter. The only notable departure from this is found among material from northern Borneo where the fruit, of several different collections, is narrowly ovoid, 7 mm. long and 4–5 mm.

thick. This form may deserve some nomenclatorial recognition. There are, however, variations of *Tournefortia tetrandra* which I believe do merit recognition at this time. The characters which set these off from typical *T. tetrandra* may be organized as follows:

Leaves $1\frac{1}{2}$ – $2\frac{1}{2}$ times as long as broad, ovate acuminate or lance-ovate *Tournefortia tetrandra*
 Leaves $2\frac{1}{2}$ – $3\frac{1}{2}$ times as long as broad, more or less lanceolate.
 Leaves dull, east Java var. *angustifolia*.
 Leaves somewhat glossy, Ceylon var. *Walkerae*.

2A. *Tournefortia tetrandra* Blume var. *angustifolia* Moritzzi, Syst. Verzeich. 52 (1845–46).

Known only from the type-collection in eastern Java.

This variety is a peculiar plant with very dull thickish leaves that have only 3–4 pairs of primary veins evident. The secondary nervation is not discernible. I know it only from the type-collection by Zollinger (no. 939), made Dec. 17, 1842, "auf den Kalkfelsen von Kuripan."

2B. *Tournefortia tetrandra* Blume var. *Walkerae* (Clarke), comb. nov. *Tournefortia Walkerae* Clarke in Hooker, Fl. Brit. India 4: 147 (1883); Trimen, Fl. Ceylon 3: 198 (1895).

Known only from Ceylon.

This plant is simply a narrow-leaved form of the species that is confined to Ceylon. The blades are lanceolate but are quite similar to those of the species in texture, nervation, etc. The fruit and flowers are similar to the common Malaysian plant.

3. *Tournefortia Hookeri* Clarke in Hooker, Fl. Brit. India 4: 147 (1883). *Tournefortia Hookeri* var. *subtropica* Clarke in Hooker, Fl. Brit. India 4: 147 (1883).

Known only from the base and lower valleys of the Sikkim Himalayas.

SPECIMENS EXAMINED: Rangit, May 15, 1876, *Clarke* 27953 (K); Great Rangit, April 1850, *Hooker & Thompson* (K, TYPE of var. *subtropica*); Mangpu, 900 m. alt., May 1905, *Meebold* 4243 (BD); Rangbi, 1500 m., May 31, 1870, *Clarke* 11790 (K, BM); Chunbati, 600 m., June 12, 1870, *Clarke* 12024 (K, BM); Chunbati, 600 m., April 1876, *Gamble* 579 (K); below Punkabaree, *Hooker* (BD); Pancheni, 1875, *Gamble* 3370 (K); Siliguri, Jan. 1873, *Gamble* 3369 (K); Dalgaoon, mixed forest, April 9, 1893, *Haines* 358 (K); Sikkim, 1862, *Andersson* 270 (BD); Sikkim, March 1871, *Clarke* 16774 (K); Sikkim Terai, *Clarke* (K); Sikkim, *Griffith* 5928 (K).

Characterized by its slender well developed calyx-lobes and by the golden or golden-brown under surfaces of the leaves. These latter are nearly glabrous or have only scattered hairs along the dark-colored

nerves and veins. The corolla is usually 3–5 mm. long with the tube forming half (or even more) of this total length. In the var. *subtropica*, which is merely the large-flowered form of the species, the corollas become ca. 8 mm. long and the calyx-lobes only about a third as long as the tube. The species is a local one and probably worthy of recognition. It is most closely related to the form of *T. montana* described as *T. khasiana*.

4. **Tournefortia Heyneana** Wallich, Num. List no. 910¹ (1828–29), nomen; Don, Gen. Syst. 4: 369 (1837); Clarke in Hooker, Fl. Brit. India 4: 145 (1883); Gamble, Fl. Madras 893 (1923). *Tournefortia reticosa* Wight, Icones 4²: 16, tab. 1386 (1848); Wight, Spicileg. Neilgherrense 2: 83, tab. 189 (1851); Gamble, Fl. Madras 893 (1923).

Hills of southern peninsular India, about lat. 11°–13° N. and long. 76°–77° E.

SPECIMENS EXAMINED: Nilgiri Hills, April 1852, *herb. Wight 2057* (K); Devala, Nilgiris, 900 m. alt., Nov. 1884, *Gamble 15588* (K); S. E. Wynaad, Nilgiris, 900 m. alt., Nov. 1884, *Gamble 15497* (K); Wynaad, *Beddome 5437* (BM); Nadooputtah, June 1846, *herb. Wight* (K); Anamalais, *Beddome 5438* (BM); Carcoor-ghat, Nilgiris, Aug. 1887, flowers varying from $\frac{1}{8}$ – $\frac{1}{2}$ inch according to age, *Lawson* (Oxford); Coorg, *White* (Oxford); Peermade Reav (? spelling), 1350 m. alt., Dec. 1910, *Meebold 12920* (BD); without data, *herb. Wight*, probable basis of Wight's plate and the TYPE of *T. reticosa* (K); without data, *ex herb Heyne, Wallich 910¹* (herb. Wallich at Kew).

A study of Wallich's herbarium, now at Kew, shows his number 910 to consist of two different species from opposite ends of India. The label reads: "910 Tournef. Heyneana, Wall. — 1. Herb. Heyn. — 2. Pundua F. de S." The Heyne plant represents the species from the Deccan with pedicellate flowers, which is the one treated here. The plant from Pundua, collected by de Sylva, is accompanied by a large special label indicating that it was found in the "Pundouh Hills" in Jan. 1824.

Clarke describes the flowers of *T. Heyneana* as $\frac{1}{8}$ – $\frac{1}{6}$ inches (3–4 mm.) long. These measurements are evidently from the duplicate of the Wallich collections now in the general herbarium at Kew. The Heyne material in the Wallich Herbarium at Kew has corollas 9–10 mm. long. The specimens, except for flower-size, are otherwise very similar and I believe they represent minor forms of the species. Significant in this connection is the note made by Lawson on one of his specimens cited above. He states that the corolla varies from 3–12 mm. according to age! Though Don makes no mention of the corolla-size in his description, the first given to the species, we may suppose that it was the large-flowered phase since the Wallich Herbarium, then in charge of the

Linnean Society, was no doubt consulted by him. In any case, since the corolla-size is variable even within the type-collection, the chief character whereby Clarke distinguished *T. reticosa* now disappears. The two species, *T. Heyneana* and *T. reticosa*, are, I believe, trivial forms of one species and quite synonymous.

DeCandolle, Prodr. 9: 516 (1845), received only the second part of Wallich no. 910, and described this as *T. Heyneana*. His description in the Prodomus, consequently, is based upon de Sylva's specimens from Pundua. Clarke pointed out this mistake, gave a new name (*T. Candollii*) to the de Sylva collection described by DeCandolle, and properly restricted the name, *T. Heyneana*, to the peninsular species collected by Heyne.

5. *Tournefortia ovata* Wallich, Num. List no. 908 (1828); Don, Gen. Syst. 4: 369 (1837); DeCandolle, Prodr. 9: 516 (1845); Clarke in Hooker, Fl. Brit. India 4: 147 (1883).

Southern Burma and the Andaman Islands.

SPECIMENS EXAMINED: Rangoon, Aug. 1826, *Wallich* (no. 15) 908 (herb. Wallich, TYPE); Rangoon, *McClelland* (K, three collections); Andamans, April 1891, *Prain* (Cambridge); Middle Andaman, Homfray Straits, climber, 1915, *Parkinson* 297 (K); Aberden, South Andaman, *Kurz* (K, parasitized; Delessert, normal); Chauldare, South Andaman,

Characterized by its elliptical abruptly acuminate leaves, its subpedicellate flowers and its southern occurrence. The corolla becomes 8 mm. long. The calyx is only 1.5 mm. long at anthesis. The leaves are mostly rather firm in texture and are usually brown and glabrous beneath. One of McClelland's collections is consequently quite atypical in having the leaves not only thin in texture but golden-brown beneath as well. Another one of his collections is quite hairy on the lower leaf-surface. The pedicels in *T. ovata* are usually at most only 1 mm. long, though in Parkinson's material cited the pedicels become fully 2 mm. long and are quite evident.

6. *Tournefortia montana* Loureiro, Fl. Cochinch. 1: 122 (1790). *Messerschmidia montana* (Lour.) Roemer & Schultes, Syst. 4: 544 (1819). *Lithospermum viridiflorum* Roxburgh, Hort. Bengal. 13 (1814), nomen; Lehmann, Asperif. 1: 30 (1818), in synon.; Roxburgh, Fl. Indica 2: 4 (1824), description; Roxburgh, Icones ined. Kew. tab. 2120. *Heliotropium viridiflorum* (Roxb.) Lehmann, Asperif. 1: 30 (1818). *Tournefortia viridiflora* (Roxb.) Wallich, Num. List no. 907 (1828); Clarke in Hooker, Fl. Brit. India 4: 146 (1883). *Tournefortia Sampsoni* Hance, Jour. Bot. 6: 330 (1868). *Tournefortia Wightii* Clarke in Hooker, Fl. Brit. India 4: 146 (1883). *Tournefortia Rox-*

burghii Clarke in Hooker, Fl. Brit. India 4: 146 (1883). *Tournefortia viridiflora* var. *Griffithii* Clarke in Hooker, Fl. Brit. India 4: 146 (1883). *Tournefortia Candollii* Clarke in Hooker, Fl. Brit. India 4: 146 (1883). *Tournefortia khasiana* Clarke in Hooker, Fl. Brit. India 4: 147 (1883). *Tournefortia Boniana* Gagnepain, Not. Syst. 3: 33 (1914) and in Lecomte, Fl. Gén Indo-Chine 4: 217 (1914). *Tournefortia Gaudichaudii* Gagnepain, Not. Syst. 3: 34 (1914) and in Lecomte, Fl. Gén. Indo-Chine, 4: 217 (1914). *Tournefortia Heyneana* sensu DeCandolle, Prodr. 9: 516 (1845).

In the hills, up to 1500 m. alt., in Assam, Upper Burma, northern Siam (Payap and Maharat), middle and northern Indo-China (Anam, Laos and Tonkin) and southern-most China (Yunnan, Kwangsi and Kwangtung).

This species presents a number of diverse phases resulting from combinations of variations in leaf-size, abundance and distribution of pubescence, and size of corolla-tube. These phases have been treated as "species" but their variability, their erratic distribution, and their occurrence together in various localities lead me to believe they are merely further manifestations of the surprising intraspecific variability of these structures among the Old World *Tournefortiae*. After discounting these variations as mere phases, I am struck with the naturalness of the distribution of the resulting aggregate species. The distribution is of the pattern found in numerous species of other genera and families inhabiting this part of Asia.

The type of *T. montana* has not been examined. Its source is not given, but the probabilities are that it came from Anam. Dr. E. D. Merrill, who has devoted much time to the consideration of Loureiro's writings, informs me that he knows no reason for doubting Loureiro's generic attribution in the present case. After a study of the description I am perfectly content to accept Loureiro's name for this species. The leaves are given as ovate-lanceolate and glabrous. Unfortunately, however, no information is given as to the shape or size of the corolla-tube.

The second name applied to our species is *Lithospermum viridiflorum*. It first appears in 1814 as a name in a list of the Calcutta Garden and is given as collected by Roxburgh at Chittagong. It was no doubt this same garden material that was described in 1824 by Wallich in Roxburgh's Flora and is now represented in Wallich's herbarium (no. 907). It is also the plant represented in Roxburgh's unpublished plates (no. 2120) now preserved at Kew. The first description of the plant, as *Heliotropium viridiflorum*, is that by Lehmann in 1818. His material also seems to have come from the Calcutta Garden. Hence, there is

every reason for taking the material grown at Calcutta as typical. This is a form characterized by distinctly lanceolate leaves that are velvety all over beneath and by small strigose corollas. The corolla-tube is 2-3 mm. long, usually densely strigose and commonly only twice the length of the calyx or less. This form has not been collected about Chittagong. As Clarke has indicated, l. c. 146, the common form of *T. montana* about Chittagong, particularly in the region in which Roxburgh is known to have collected, is the plant with long corolla-tubes described by Clarke as *T. Roxburghii*. As matters stand, therefore, we may either believe that Roxburgh did not collect his plant at Chittagong, or that having collected the common long-tubed *Tournefortia* there it subsequently became a short-tubed form under garden conditions. I have seen material of the type-form of *T. viridiflora* from Assam, Burma and Siam.

The type of *T. viridiflora* var. *Griffithii* is a collection made in the Khasia Hills by Griffith. It differs from the type-form of *T. viridiflora* in having the leaves much less hairy or nearly glabrous beneath and corollas that are possibly a trifle larger. The type of *T. Boniana* collected by Bon (no. 1932) at O-cach, on the mountain Ma-dong in Indo-China, is quite similar. I have seen this glabrescent small-flowered form from Assam, Burma and Indo-China.

In publishing *T. Wightii*, Clarke gave its source as "Deccan Peninsula, Wight." The type is Wight no. 2056 and is accompanied with one of the old printed labels indicating that it was part of the Wight materials handled at Kew in 1866-67. The label proper is headed "Peninsula Indiae Orientalis." We may accept that no. 2056 was part of the Wight Herbarium but as to the collector of the specimen and its original source doubt must remain. Since the plant agrees closely with plants from Burma I suspect that perhaps it came from that general region and may represent material received by Wight from Roxburgh or some other collector of that period. Gamble, Fl. Madras, 894 (1923), reports the species from the Anamalai Hills, Madras. The only *Tournefortia* I have seen from that general region is *T. Heyneana*! Until undoubted material from Southern India is forthcoming I believe that *T. Wightii* should be accepted as clearly applying to the material east of the Ganges here discussed. In the type-form of *T. Wightii* the leaf-surface is velvety beneath much as in typical *T. viridiflora*. The corolla is much larger, however, with the tube 2-4 times as long as the calyx. *Tournefortia Roxburghii* is a form of *T. Wightii* which has lanceolate rather than ovate leaf-blades. It is a rather common form. I have seen plants similar to the type-form of *T. Wightii* and *T. Roxburghii* from throughout the range of *T. montana*.

Tournefortia Candollii is based upon "*T. Heyneana*, DC. Prodr. ix. 516; Wall. Cat. 910, as to the Khasia examples." In the Wallich Catalogue no. 910 consists of two parts, 1. material from Heyne, the type of *T. Heyneana* Wall. and 2. material collected by de Silva at Pundua. DeCandolle's specimen of *Wallich 910* consists only of the second part of the Wallich number, that is to say, the material from Pundua by de Silva. This specimen was described by DeCandolle as *T. Heyneana*. Clarke, l. c. 145, recognizing that the name *T. Heyneana* was obviously to be associated with Heyne's material from southern India, gave a new name, *T. Candollii*, to the plant improperly described as *T. Heyneana* by DeCandolle. The type of *T. Candollii* is accordingly de Silva's material in the DeCandollean Herbarium. The specimen at Geneva is broken and poor but has good corollas. These are somewhat constricted at the throat and very similar to those found in the type of *T. khasiana*. The leaves are lanceolate, dried brown beneath and nearly black above. They are very sparsely strigose above and have only scattered hairs along the principal veins beneath.

I consider *T. Candollii* to be the form of *T. montana* with elongate corolla-tubes and glabrescent leaves. Belonging with it are several further synonymous forms. The type of *T. Sampsoni* is from Sai-chü-shan caverns in the province of Kwangtung and is now deposited at the British Museum. There is some interesting variation within this collection. The corolla-tube is medium to long (5–8 mm.) and the lanceolate leaves are either distinctly appressed hairy or are quite glabrous beneath. The type of *T. khasiana* was collected by Clarke (no. 15227) at Nonpriang in the Khasia Hills. It is a form of *T. Candollii* in which the corolla-tube is contracted upward toward the throat so that the throat is at times almost half the diameter of the base of the tube. The type of *T. Gaudichaudii* is a glabrescent plant with elongate corollas and broadly lanceolate leaves. It was collected in Anam (Tourane) by Gaudichaud.

7. *Tournefortia luzonica* sp. nov., scandens grisea; ramulis obscure tetragonis 2–4 mm. crassis pilis numerosis brevibus divergentibus vestitis; foliis oppositis vel suboppositis; petiolis 5–14 mm. longis; lamina folii ovata vel late lanceolata 5–13 cm. longa 2–7 cm. lata apice breviter acuminata basi rotunda vel (1–4 mm. profunde) cordata, supra pilis rigidulis brevibus ascendentibus plus minusve numerosis vestita, subtus pallidiore pilis gracilibus falcatis saepe numerosis vestita nervis 6–9-jugatis ornata; inflorescentia hispidula; calycibus sessilibus 1–2.5 mm. altis, lobis anguste lanceolatis vel linearibus erectis; corolla virescentibus, tubo 2–4(–8) mm. longo, limbo 2–2.5 mm. lato; fructu globoso

3–4 mm. diametro albo glaberrimo succoso; nuculis 2 biovulatis laevibus.

Endemic to the Philippines where it is confined to the mountainous regions of northern, east-central and southern Luzon.

SPECIMENS EXAMINED: vicinity of Peñablanca, Cagayan Prov., a vine on hillside, fl. green, fruit white, May 3, 1917, *M. Adduru 237* (TYPE, herb. Arnold Arboretum; isotype, Kew); Peñablanca, 1926, *Ramos & Edaño 46663* (BM); Bangui, Prov. Ilocos Norte, *Ramos 27563* (BM); Burgos, Prov. Ilocos Norte, *Ramos 4799* (BD); Bocana del Abra, Prov. Ilocos Sur, *Micholitz* (K); Mt. Pulog, Mountain Prov., Jan. 1909, *Curran, Merrill & Zschokke 16103* (BD); Benguet, *Loher 1541, 1542* (K); dist. of Lepanto, Mountain Prov., *Vidal 3326* (K); Baguio, Benguet, *Elmer 8467* (AA, K); Mt. Maquilong, Prov. Batangas, *Vidal 3327* (K); Prov. Albay, *Cuming 1215* (K, BM, BD).

7A. *Tournefortia luzonica* var. *sublucens*, var. nov., a forma typica speciei differt foliis sparse inconspicueque pubescentibus, supra vix griseis sed subluculentibus.

Confined to the mountains of west-central Luzon.

SPECIMENS EXAMINED: Anuling, Zambales Prov., 1924, *Ramos & Edaño 44553* (TYPE, herb. Arnold Arboretum; isotypes, Kew, Brit. Mus.); Zambales, 1907, *Ramos 4799* (BD); Lamao, Mt. Mariveles, Bataan Prov., *Meyer 2844* (K, BD); Lamao River, Mt. Mariveles, 350 ft. alt., slender vine growing over trees for many yards, *Williams 525* (K).

Among all the Old World species of *Tournefortia* this species is unique in the possession of opposite or subopposite leaves. In the treatments of the Philippine *Boraginaceae* by Robinson, Philip. Journ. Sci., Bot. 4: 694 (1909), and by Merrill, Enum. Philip. Pl. 3: 376 (1923), this plant has generally passed as *T. Horsfieldii* Miquel. That species, however, with its alternate leaves and a fruit composed of four uniovulate nutlets is one of the forms of the widely ranging *T. sarmentosa*.

The var. *sublucens* is confined to the mountainous country of west central Luzon, prov. Bataan and Zambales, and seems to have a range quite distinct from the typical form of *T. luzonica* which ranges in the other parts of the island of Luzon. Essentially a glabrate form of *T. luzonica*, with the upper leaf-surfaces more or less glossy, it is significant and worthy of nomenclatorial recognition only if it has a range apart, and is geographically correlated.

8. *Tournefortia Muelleri*, nom. nov. *Tournefortia mollis* F. v. Mueller, Frag. 1: 59 (1858); Bentham, Fl. Austral. 4: 390 (1869); Bailey, Queensland Fl. 4: 1041 (1901); not *T. mollis* Bertol. (1852).

Northern Australia and Papua.

SPECIMENS EXAMINED: Edgecombe Bay, Queensland, *Dallachy* (K); along Burdekin River, *Mueller* (K, isotype); Herbert River, *Dallachy*

(K); Cape York Peninsula Exped., *Hann 146* (K); shores of Montague Sound, W. Australia, 1820, *Cunningham 182* (K, BM) and *324* (BM); erect shrub 1.5–2 m. tall, fringing tidal areas, Kapa Kapa, Papua, *Brass 505* (AA, K); Port Moresby, Papua, 1918, *White 6* (AA).

The carpels seem to be more bony than in other Old World species of this section. The leaves are usually lanate.

9. *Tournefortia puberula* Baker, Jour. Linn. Soc. London, **20**: 211 (1883). *Tournefortia Mocquerysi* A. DeCandolle, Bull. Herb. Boiss. ser. 2, **1**: 581 (1901).

Forests of eastern Madagascar and the Seychelles. Possibly introduced in the latter archipelago.

SPECIMENS EXAMINED: MADAGASCAR: forests east of Ivohibé, 1000 m. alt., fl. white, Nov. 3, 1924, *Humbert 3163* (P); high valley of the Rienana, drainage of the Matitana, 1000–4000 m. alt., fl. white, Nov. 1924, *Humbert 2523* (P); Central Madagascar, *Baron 1957* (Kew, TYPE of *T. puberula*; BM, BD, isotypes), *2798* (K, BM, P), *3106* (K, P) and *6991* (K); forest of Ivohimanitra, Nov. 8, 1894, *Forsyth Major 64* (K, BM, BD, P); forest of Analamazaotra near col d'Amboasary, ca. 950 m. alt., shrub with white flowers, Oct. 23, 1912, *Viguietto & Humbert 978* (P); forest at head of Antongil Bay, a liana with white flowers, *Mocquerys 161* (Deles., TYPE of *T. Mocquerysi*). SEYCHELLES: Mahé, common shrubby climber in hills near streams, Sept. 1871, *Horne 247* (K); Mahé, *Thomasset* (K); Mahé, *Thomasset 10* (BM); Mahé, 1867, *Wright* (BM); Terné, Mahé, 1908, *Gardiner* (K); Silhoutte, common in cultivation, 1908, *Gardiner 113* (K); indefinite, a twining shrub generally on rocks near rivers, May 1902, *Thomasset 22* (K, BM).

The types of *T. puberula* and *T. Mocquerysi* are quite indistinguishable. The species is a readily recognizable one. The leaves are firm, apparently glabrous and the stems are covered with a minute brownish puberulence. There is both a short- and a long-corolla form. The plant of the Seychelles is certainly identical with that of Madagascar. Possibly it represents a horticultural introduction to the islands. In accounts of the Seychelles flora, Baker, Fl. Mauritius and Seychelles 202 (1877), and Summerhayes, Trans. Linn. Soc. London, Zoölogy, **19**: 284 (1931), the species has consistently been misdetermined as *T. sarmentosa*.

9A. *Tournefortia puberula* var. *Kirkii*, var. nov., a varietate genuina differt pilis brevibus pallidis adpressis ornatis.

Islands off the northwest coast of Madagascar.

SPECIMENS EXAMINED: Mohilla Island, Comoro Archipelago, April 1861, *J. Kirk* as "*Tournefortia* (3)" (TYPE, herb. Kew); Nossi-bé, June 1847, *Boivin 2086* (P); Nossi-bé, 1853, *Perrille* (P).

This variety comes from a much more arid region than typical *T.*

puberula and may be only a hairy xerophytic form of that species. In typical *T. puberula* the plant is provided with a minute, frequently somewhat golden puberulence. In the var. *Kirkii* the stems have a sparse pale short strigosity that tends to disappear with age. The petioles are sparsely strigose. The lower surface of the leaf-blades has short white closely appressed hairs scattered along the rib and veins. The upper surface is somewhat strigose but less abundantly so than below. The inflorescence has numerous short ascending pale hairs.

10. *Tournefortia acuminata* DeCandolle, Prodr. 9: 520 (1845); Cordemoy, Fl. Réunion 479 (1895).

Endemic to the Island of Reunion (Bourbon).

SPECIMENS EXAMINED: les hauts du Boucan Launay, *Boivin* 1241 (K, BD, DC, Boiss, P); Bébou au dessus de la plantation de Quinquinas, July 28, 1875, *G. de l'Isle* 499 bis (K, Coss.); Bourbon, arbor, [? *Commer-son*] (herb. Smith); chemin que conduit de Sante Rose à Saint Joseph avant la descente qui conduit au Volcan, 1812, *Commerson* (P); "l'île de France au bourbon," *ex Mus. Paris* (TYPE, herb. DC).

The type of *T. acuminata* at Geneva is given as distributed from Paris in 1821 and as from either Reunion or Mauritius. It represents a form in which the stems, petioles and inflorescence are glabrous or only very scantily strigose. It is obviously a duplicate of the collection at Paris which is labeled as collected by Commerson on the road between Ste. Rose and St. Joseph on Reunion. The material which I have cited from Boivin, which is widely distributed in European herbaria, is a form in which the stems, petioles and inflorescence have a short and evident, though not very abundant nor very conspicuous strigosity that becomes more or less brownish or golden. This I believe is the common form of the species. The leaves in *T. acuminata* are 12–17 cm. long and 3.5–7 cm. broad, are acute at both ends, and have 10–15 pairs of nerves. The calyx is 1.5–2 mm. long at anthesis and has erect, cuneate or more or less lanceolate lobes. The corolla-tube is 3.5–7 mm. long. The limb is ca. 4 mm. broad.

11. *Tournefortia arborescens* Lamarck, Tab. Encyc. 1: 417 (1791); Poiret, Encyc. 5: 357 (1804). *Tournefortia velutina* Smith in Rees, Cyclop. 36: sp. no. 13 (Aug. 1817!), not *T. velutina* HBK. (1818). *Tournefortia Bojeri* sensu Cordemoy, Fl. Réunion 479 (1895).

Endemic to the Island of Reunion (Bourbon).

SPECIMENS EXAMINED: Grand Bassin, Aug. 6, 1875, *G. de l'Isle* 454 (K, P); Gauteuron (spelling ?) du Gol, woods, fl. white, *Commerson* (herb. Smith, TYPE of *T. velutina*); Reunion, *Commerson* (herb. Smith,

second sheet of *T. velutina*), Bory (Deles) Boivin (BD) and Guyot 431 (BD); "in Mauritius," herb Bojer as *T. bifida* (BM); "de l'inde" [? Sonnerat] (Paris, TYPE of *T. arborescens*).

The type material of *T. arborescens* is accompanied by a small label reading: "Tournefortia d l'inde." The collector is not indicated but both Lamarck and Poiret attribute it to Sonnerat who visited the Mascarenes during his voyage to India and Malaysia. The material consists of two sheets, one bearing a sterile shoot with entire oblanceolate leaves more or less tomentose beneath in the manner common in the spicate *Cordia* species of the section *Varronia*. The second sheet contains a *Tournefortia* in flower. The latter is a form of the species as here defined, having the leaves only very sparsely and obscurely strigose, particularly above. The stems bear numerous but not very abundant short appressed pale hairs. The calyx-lobes are ovate, acute and sparsely pale strigose. The specimen evidently represents the sparsely hairy form of the endemic species of Reunion.

The type of *T. velutina* is the form of the species with very abundant long hairs. It has the leaves pale and silky with a dense indument of slender very pale hairs. The calyx lobes are ovate, densely hairy and more or less golden tawny. Smith mentioned atypical material of his *T. velutina* from Mauritius, but this, in fact, represents a form of *T. Bojeri*. DeCandolle, Prodr. 9: 514 (1845), incorrectly cited *T. velutina* as a possible synonym of *T. argentea*. I have cited above a specimen given as collected on Mauritius by Bojer. I doubt the accuracy of the geographical data and believe that the specimen is really from Reunion. Its broad calyx-lobes are ovate or orbicular-ovate and hence similar to those found in all material indubitably from that island.

12. **Tournefortia Bojeri** A. DeCandolle, Prodr. 9: 516 (1845); Baker, Fl. Mauritius, 202 (1877). *Tournefortia bifida* sensu Bojer, Hort. Maurit. 234 (1837).

Endemic to the Island of Mauritius (Ile de France).

SPECIMENS EXAMINED: Mauritius, woods, 1837, Bojer as *T. bifida* (TYPE, herb. DC); without locality, 1839, Bouton as *T. bifida* (DC, co-type); Mauritius, mountains and forest, Bouton (K); Mauritius 1854, Boivin (K); Mauritius, 1811, Hardwick (BM); Mauritius, [Commerçon] (herb. Smith); Mauritius, Sieber 98 (BD); Mauritius, herb. Labillardière (Deles); "Bourbon," 1853, Boivin (Boiss):

Boivin's collection which it cited above and attributed to Reunion is, I believe, mislabeled. Indubitable collections of *T. Bojeri* come only from Mauritius. The species is very closely related to *T. arborescens* of Reunion, differing chiefly in the narrower calyx-lobes. In the DeCandolle Herbarium there is a branch of *T. Bojeri*, mounted on a sheet with

isotypic material of the Philippine *T. Urvilleana*. The only label accompanying this mixed sheet is in the script of Chamisso and belongs to the Philippine species. This mixed sheet makes comprehensible DeCandolle's, Prodr. 9: 515, adnot. (1845), strange comparison of *T. Bojeri* and *T. Urvilleana*. Since Chamisso never visited the Mascarenes it is evident that the spray of *T. Bojeri* has somehow become divorced from its proper label. The name "*T. cymosa* Heyne" seems to be based upon material from Mauritius. For a discussion of this *nomen* see my list of doubtful and excluded species on p. 166.

In *T. Bojeri* the stems, petioles and inflorescence are more or less velvety with a pale ascending or spreading (or very rarely appressed) usually abundant hairs. The leaf blade is acute at both ends, more or less strigose on both surfaces though usually less so above. It has 10–12 pairs of veins and is 11–17(–24) cm. long and 2–5(–6) cm. broad. The calyx is 2–2.5 mm. long and has the lobes cut at least $\frac{3}{4}$ way to base. It is more or less silky strigose. The lobes are lanceolate to broadly lanceolate or cuneate-lanceolate. The corolla-tube is 2–8 mm. long, and 2–5 times the length of the calyx. The corolla-limb is 2–3 mm. broad. The fruit is ca. 3 mm. in diameter.

Messerschmidia Linnaeus ex Hebenstreit, Nov. Comment. Acad. Sci. Imp. Petrop. 8: 315, tab. 11 (1763); Gmelin, Fl. Sibir. 4: 77 (1769); Murray, Syst. Nat. ed. 13, 161 (1774); Linnaeus fil. Suppl. Pl. 132 (1781). — type-species, *Tournefortia sibirica* Linn. *Messerschmidia* Linnaeus, Hort. Upsal. 36 (1748); Linnaeus, Mant. 1: 5 and 42 (1767); Linnaeus, Syst. ed. 12, 149 (1767); Linnaeus, Mant. 2: 334 (1771). — a variant spelling of *Messerschmidia*, type-species, *Tournefortia sibirica* Linn. *Tournefortia* sect. *Messerschmidia* (Linn.) DeCandolle, Prodr. 9: 528 (1845); as to nomenclatorial type only, not as to the species of *Heliotropium* treated. *Argusia* Amman, Stirp. Rar. Ruth. 29 (1739). *Arguzia* [Amman] Rafinesque, Sylva Tellur. 167 (1838); Steven, Bull. Soc. Nat. Moscow 24¹: 558 (1851). — type-species, *Tournefortia sibirica* Linn. *Tournefortia* sect. *Arguzia* [Amman] DeCandolle, Prodr. 9: 514 (1845); Ledebour, Fl. Ross. 3: 97 (1847–49). — type-species, *Tournefortia sibirica* Linn. *Tournefortia* sect. *Mallota* A. DeCandolle, Prodr. 9: 514 (1845). — type-species, *T. argentea* Linn. *Tournefortia* sect. *Mallotonia* Grisebach, Fl. W. Ind. 483 (1861). — type-species, *Tournefortia gnaphalodes* R. Br. ex R. & S. *Mallotonia* (Griseb.) Britton, Ann. Mo. Bot. Gard. 2: 47 (1915). — type-species, *Tournefortia gnaphalodes* R. Br.

Segregated here, as the emended genus *Messerschmidia*, are three

remarkable species that depart widely in appearance from the numerous and habitually very uniform species formerly associated with them in *Tournefortia*. As I have redefined and amplified *Messerschmidia* it consists of the original Asiatic herb, *Tournefortia sibirica*, the strand-shrub of the Antilles, *T. gnaphalodes*, and the well known strand-tree of the Indian and Pacific oceans, *T. argentea*. All these species differ widely not only in their habit of growth and in their selection of habitat from all the other species that have been traditionally placed with them in *Tournefortia*, but also in their pronounced development of a corky exocarp which sets them off not only from all species of *Tournefortia* but from all other *Boraginaceae* as well. All three of the species show a marked preference for saline conditions. Two of them are tropical strand-plants. The third species grows along the ocean in temperate eastern Asia, in more or less saline soils along streams and about inland seas in Central Asia and eastern Europe. The corky exocarp evidently adapts the three species for water dispersal. The nature of the hairy covering of these three species is of an essentially similar type, consisting of slender silky hairs rather different in texture and appearance from that predominating among the species of true *Tournefortia*.

The generic name *Messerschmidia* (also spelled *Messersmidia* and *Messerschmidtia*) is based upon *Tournefortia sibirica* Linn., and is a synonym of *Argusia* (or *Arguzia*). The type-species was first described by Amman in 1739 who applied to it the monomial, *Argusia*, and gave a lengthy description of it based upon notes and specimens made by D. G. Messerschmid in 1724 along what is now the northwestern frontier of Manchuria. The source of this material is given as "Locus in glareosis aridisque apricis Argun fluuii et Iike Dalai Noor in Dauria." Although Amman's monomial was formed from the "loco natali" of the plant, i.e. the Argun River, its author deliberately and repeatedly spelled it "*Argusia*"! Amman states that seeds from Messerschmid's collection germinated and grew in the gardens at St. Petersburg. These same cultures are probably those described and illustrated by Hebenstreit in 1763. The plants growing in the Upsala Garden in 1748 and described by Linnaeus as *Messersmidia* were probably derived from those grown by Amman. In the Correspondence of Linnaeus, ed. Smith 2: 200 (1821), there is a letter from Amman, dated Nov. 18, 1740, in which questions by Linnaeus concerning *Argusia* are answered and in which it is stated that dried specimens of *Argusia* were being sent him. When he proposed the monomial "*Argusia*," Amman justified his use of a geographic appellation in forming the name, but added that he had no objection if the genus was named after Messerschmid, its original col-

lector. Linnaeus seems to have preferred the latter. The collector's name was spelled "Messerschmid" by his contemporaries. Linnaeus latinized it, "*Messerschmidia*," and was consistent in this usage in all his writings. Other writers of the last half of the 18th century, however, spelled it "*Messerschmidia*" and it is so spelled in the paper by Hebenstreit who was the first to use the generic name subsequent to 1753. Writers of the past century tended to spell the generic name "*Messerschmidtia*." The generic name *Messerschmidia* has variant spellings in "*Messerschmidia*" and "*Messerschmidtia*." Although clearly based upon, in fact named after the original collector of *Tournefortia sibirica*, the generic name *Messerschmidia* (variously spelled) eventually became associated with two other very diverse groups of *Boraginaceae*. A study of the facts here presented, however, makes it evident that the name "*Messerschmidia*" is only very improperly applied either to the American species of *Tournefortia* sect. *Cyphocyema*, or to Canary Island and South African species of *Heliotropium* as has been done in some large works. In another paper, Contr. Gray Herb. 92: 73 (1930), I have given many facts concerning the misuse of the name "*Messerschmidia*." The name was based upon *Tournefortia sibirica* and was originally applied solely to that plant. The type-species of *Messerschmidia* is obviously and logically the original Siberian species.

KEY TO THE SPECIES

- Plant a low herb from rhizomes; inflorescence a loose open corymbose cyme; calyx pedicellate, lobes cuneate; anthers several times as long as broad; fruit pubescent, sunken in at apex; carpels embedded in the center of the corky exocarp; temperate Eurasia1. *M. sibirica*.
- Plant a tree or shrub; inflorescence of scorpioid cymes; calyx sessile, lobes orbicular or oblong; anthers about two times as long as broad; fruit glabrous, apex conic or rounded; carpels occupying the apical half of the fruit, the lower half composed entirely of corky exocarp; tropical strand plants.
- A tree 1-5 m. tall; leaves broadly oblanceolate or obovate, 3.5-9 cm. broad; inflorescence a conspicuous stiff panicle of loosely flowered elongating (up to 8 cm.) scorpioid cymes; corolla-lobes merely imbricate (not plicate) in the bud; anthers partially exerted from the short corolla-tube; fruit dull, breaking in half; apex and dorsal surface of carpels covered with corky exocarpial tissue; tropics of the Old World2. *M. argentea*.
- A shrub 3-12 dm. tall; leaves narrowly spatulate-linear, 4-10 mm. broad; inflorescence consisting of single or paired long-peduncled very congested short (1-2 cm.) scorpioid cymes; corolla-lobes distinctly plicate in bud; anthers well

included in the cylindrical corolla-tube; fruit brown and lustrous, not breaking in half; apex and dorsal surface of carpels not covered with corky exocarpial tissue; West Indies3. *M. gnaphalodes*.

1. *Messerschmidia sibirica* Linnaeus, Mant. 2: 334 (1771). *Tournefortia sibirica* Linnaeus, Sp. Pl. 141 (1753); Kusnezow & Popow, Fl. Caucas. Crit. 4²: 77 (1913). *Messerschmidia Argusia* Linnaeus, Mant. 1: 42 (1767). *Messerschmidia Argusia* Murray, Syst. Nat. ed. 13, p. 161 (1774); Linnaeus fil. Suppl. Pl. 132 (1781). *Messerschmidia Argunia* Gaertner, Fruct. 2: 130, tab. 109 (1791). *Tournefortia Argusia* (L.) Roemer & Schultes, Syst. 4: 540 (1819); Ledebour, Fl. Ross. 3: 97 (1847-49); Herter, Act. Hort. Petrop. 1: 503 (1872). *Messerschmidia rosmarinifolia* Willdenow ex Roemer & Schultes, Syst. 4: 544 (1819). *Tournefortia rosmarinifolia* Willdenow ex Steudel, Nomen. ed. 2, 2: 693 (1841). *Tournefortia Argusia* var. *rosmarinifolia* (Willd.) Turczaninow, Bull. Soc. Nat. Moscow 23¹: 498 (1850). *Argusia rosmarinifolia* Steven, Bull. Soc. Nat. Moscow 24¹: 559 (1851). *Argusia repens* Rafinesque, Sylva Tellur. 167 (1838). *Tournefortia Argusia* var. *latifolia* DeCandolle, Prodr. 9: 514 (1845); Turczaninow, Bull. Soc. Nat. Moscow 23¹: 498 (1850). *Tournefortia Argusia* var. *angustior* DeCandolle, Prodr. 9: 514 (1845); Turczaninow, Bull. Soc. Nat. Moscow 23¹: 498 (1850). *Tournefortia sibirica* var. *angustior* Turczaninow ex Fedtchenko, Consp. Fl. Turkestan 5: 39 (1913). *Tournefortia Argusia* var. *cynanchoides* Turczaninow ex Steven, Bull. Soc. Nat. Moscow 24¹: 559 (1851), in synon. *Argusia Messerschmidia* Steven, Bull. Soc. Nat. Moscow 24¹: 560 (1851). *Argusia cimmerica* Steven, Bull. Soc. Nat. Moscow 24¹: 560 (1851). *Heliotropium japonicum* Gray, Mem. Amer. Acad. ser. 2, 6: 403 (1859).

From Japan, Amur and northern China across Asia, mostly between lat. 40° and 55° N., to Rumania and central Russia; affecting moist gravelly, usually saline soils. For more details on distribution see Ledebour, Fl. Ross. 3¹: 97 (1847-49); Herter, Act. Hort. Petrop. 1: 503 (1872) and Kusnezow & Popow, Fl. Caucas. Crit. 4²: 78 (1913).

2. *Messerschmidia argentea* (Linnaeus), comb. nov. *Tournefortia argentea* Linnaeus fil., Suppl. Pl. 133 (1781). *Tournefortia arborea* Blanco, Fl. Filip. 129 (1837).

A strand-tree widely distributed within the tropics, on islands in the Indian and Pacific oceans.

The distribution of this species is worthy of a detailed statement. The fruit having a corky exocarp is admirably suited for oceanic dispersal. In this it has been very successful. The species is, in fact, one of the

characteristic strand-plants of the Old World Tropics. It is, however, almost exclusively a plant of island-shores. In the Pacific Ocean it ranges from the Paumotu (Ducie Isl.), the Marquesas and Palmyra Island, westward to Bonin Island, the Liu Kiu Islands, Formosa, Tizard Reef (China Sea), "Annam (Turan)," the Philippines, the Moluccas, Timor, tropical Australia, and New Caledonia. In the Indian Ocean it extends from northwestern Australia, Timor and Java, Christmas and Cocos Keeling islands to the Mascarenes, Madagascar (near south end only) and coast of Mozambique (rare), north to Zanzibar, the Seychelles, the Laccadives (Bitrapar in lat. $11^{\circ}30'$ N.), the Maldives, Ceylon, the Andamans (Great Coco Isl. in lat. 14° N.), the Nicobars, the islands (Vogel, lat. $7^{\circ}46'$ N.; Adang calat, lat. $6^{\circ}30'$ N.) off the west coast of peninsular Siam, and the northwestern Federated Malay States ("Kedah"). Miquel, Prodr. Fl. Sumatra, 244 (1855), reports it vaguely from Sumatra. I have seen no material from Sumatra, Borneo or the Celebes. Except for the record from Indo-China and the vague record for the Malay States the species is not known from the Asiatic continent. In Africa it is reported only from the Mozambique Coast. The record for Amboland (*Schinz* 757), found in the Flora of Tropical Africa, 4²: 30 (1905), is evidently a clerical error for the specimen cited is *Heliotropium tuberculosum*!

The original description of *T. argentea* is based upon material collected on the coast of Ceylon by König. In the Linnean Herbarium there is a characteristic specimen of this plant accompanied by König's label reading "habitat ad Littora maris Zeylanica." Accompanying this is a label in the script of the younger Linnaeus reading "Konig, 1777." The *Buglossum lanuginosum* of Rumphius, cited by the younger Linnaeus, is evidently conspecific with König's material from Ceylon. DeCandolle, Prodr. 9: 514 (1845), cites *T. velutina* Smith as a possible synonym of *T. argentea*. Smith's plant, however, is a very different species being a synonym of *T. arborescens* Lam. of Reunion.

3. **Messerschmidia gnaphalodes** (Linnaeus), comb. nov. *Heliotropium gnaphalodes* Linnaeus, Syst. ed. 10, p. 913 (1759) and Amoen. Acad. 5: 394 (1760). *Tournefortia gnaphalodes* (L.) R. Brown ex Roemer & Schultes, Syst. 4: 538 (1819). *Mallotonia gnaphalodes* (L.) Britton, Ann. Mo. Bot. Gard. 2: 47 (1915).

A strand-plant widely distributed in the West Indies.

According to Millspaugh, Publ. Field Mus., Bot. 2: 89 (1900), this species grows "On the beach line facing the open sea, [and is] very seldom, if ever, found in bays or where partially dry reefs guard the

shore." Its range may be stated as follows: Bermuda, the Bahamas (north to about lat. 27° N.), southern peninsular Florida (to Miami region) and the Greater Antilles, southward to Granada (in the Lesser Antilles), the islands off Venezuela, the Paraguaná Peninsula of north-western Venezuela (Medanos Isthmus) and westward to Alacran Reef (north of Yucatan), the coasts of Yucatan, Cozumel Island, and Swan Island (off Honduras). The species has been reported from the "Society Islands" in Polynesia by Hooker & Arnott, Bot. Beechey Voy. 67 (1832), but as Drake, Fl. Polynés. Franç. 130 (1893), has stated this is probably the result of some error. This West Indian species is certainly not to be expected in the South Pacific.

This species was founded by Linnaeus entirely upon an illustration and phrase-name given by Plukenet, Phytogr. tab. 193, fig. 5 (1691). This basic phrase-name is as follows: "*Heliotropium gnaphaloides litoreum frutescens Americanum Sea Lavender, Barbadosibus dictum.*" From it we may suppose that Plukenet's material came from the Barbados.

DOUBTFUL AND EXCLUDED NAMES

Tournefortia angustifolia (Lam.) Roemer & Schultes, Syst. 4: 539 (1819). — *Heliotropium messerschmidioides* Kuntze.

Tournefortia angulosa Desfontaines, Tab. ed. 2, 85 (1815). — A bare name in a garden-list.

Tournefortia bifida Lamarck, Tab. Encyc. 1: 417 (1791); Poiret, Encyc. 5: 360 (1804); Poiret, Dict. Sci. Nat. 41: 177 (1826); Smith in Rees, Cyclop. 36: sub sp. no. 25 (1819); Baker, Fl. Mauritius, 202 (1877). — The type of this species was collected on l'Ile de France by Commerson and represents *Antirhea frangulacea* DeCandolle, Prodr. 4: 460 (1830)! The correct name for this Mauritian species of *Rubiaceae* is, accordingly, ***Antirhea bifida*** (Lam.), comb. nov.

"***Tournefortia cymosa*** Heyne in Herb. Rottler, not of Linn." ex Clarke in Hooker, Fl. Brit. India 4: 145 (1883). — This reference concerns a small specimen at Kew which may possibly represent *T. Bojeri* of Mauritius. It is certainly not *T. Heyneana* as given by Clarke! The specimen bears a printed label reading: "Herbarium Rottlerianum; Penins. Indiae Orientalis; Presented by the Council of Kings College, Feb. 1872." Accompanying this are two labels in script giving the determination as *T. cymosa* Swartz and the collector as Macé. Clarke's citation accordingly is merely a reference to a misdetermined specimen in the Kew herbarium.

Tournefortia Edgeworthii A. DeCandolle, Prodr. 9: 529 (1845). — *Heliotropium zeylanicum* Burman.

Tournefortia fruticosa (Linn. f.) Ker, Bot. Reg. 6: tab. 464 (1820). — *Heliotropium messerschmidioides* Kuntze.

Tournefortia linearis E. Meyer in Drege, Flora 26²: Beigabe p. 57 and 226 (1843), nomen. — *Heliotropium lineare* (E. Meyer) Wright.

Tournefortia Messerschmidia Sweet, Hort. Suburb. London 31 (1818), nomen subnudum. — *Heliotropium messerschmidioides* Kuntze.

Tournefortia micranthos (Bunge) A. DeCandolle, Prodr. 10: 67 (1846); Ledebour, Fl. Ross. 3: 98 (1847–49). — *Heliotropium micranthos* (Bunge) Boissier.

Tournefortia mollis A. Bertoloni, Misc. Bot. 12: 44, tab. 1 (1852). — Based upon material from Mozambique representing *Vangueria tomentosa* Hochst. This species of Bertoloni's is not mentioned in Robyn's recent monograph of *Vangueria*, Bull. Jard. Bot. Brux., vol. 11 (1928).

Tournefortia mutabilis Ventenat, Choix Pl. tab. 3 (1803). — The basis of this species was given by Ventenat as follows: "Arbrisseau originaire de Java, cultivé chez Cels et au Muséum d'Histoire Naturelle, de semences rapportées par La Haye." I have seen Ventenat's original material in the Delessert Herbarium at Geneva and duplicates of it at Kew, Berlin and Paris. The plant is evidently not a species of the Old World, in fact, it appears to be a form of the Mexican *T. Hartwegiana* Steud. Since Ventenat's name is much older than *T. Hartwegiana* it must be taken up in place of the latter. La Haye (or Lahaia) was a gardener who travelled to the East Indian Islands collecting seeds and plants which were subsequently grown at the garden of J. M. Cels and at the Jardin des Plantes at Paris. Since he is not known to have visited America it is evident that all of Ventenat's original data are incorrect.

Tournefortia Royleana DeCandolle, Prodr. 9: 527 (1845). — *Heliotropium zeylanicum* Burman.

Tournefortia stenoraca Klotzsch in Peters, Reise Mossamb. 250 (1861). — *Heliotropium zeylanicum* Burman.

Tournefortia subulata Hochstetter ex DeCandolle, Prodr. 9: 528 (1844). — *Heliotropium zeylanicum* Burman.

Tournefortia tuberculosa Chamisso, Linnaea 4: 467 (1829). — *Heliotropium tuberosum* (Cham.) Gürke.

Tournefortia zeylanica (Burman) Wight, *Illust. Ind. Bot.* 2: 211, tab. 170 (1850). — *Heliotropium zeylanicum* Burman.

Messerschmidia angustifolia Lamarck, *Tab. Encyc.* 1: 415 (1791). — *Heliotropium messerschmidioides* Kuntze.

Messerschmidia cancellata d'Asso, *Synop. Aragon.* 21, tab. 1 (1779). — *Rochelia* species.

Messerschmidia floribunda Salisbury, *Prodr.* 112 (1796). — *Heliotropium messerschmidioides* Kuntze.

Messerschmidia fruticosa Linnaeus fil. *Suppl.* 132 (1781). — *Heliotropium messerschmidioides* Kuntze.

Messerschmidia hispida Benthham in Royle, *Ill. Bot. Himal. Mts.* 306 (1836). — *Heliotropium zeylanicum* Burman.

Heliotropium pannifolium Burchell ex Hemsley, *Voy. Challenger, Bot.* 2: 78 (1884). — This species from St. Helena is known only from Burchell's material. It is now probably exterminated. I have studied Burchell's unpublished drawing of the plant and his specimen at Kew. The plant is evidently a strong shrub much resembling the *Eutournefortiae* of the Andes in foliage and habit of growth. I know of no *Heliotropium* that could be recognized as a close relative of it nor one that could be said to resemble it in gross habit. Burchell's specimen is in the flowering condition only. The corollas, most unfortunately, have been almost completely eaten away by insects. There are consequently no reproductive structures on the type which might help in definitely placing the St. Helena plant generically. Since the plant is no doubt extinct and no further specimens are to be expected, the species will probably remain one of dubious generic affinities, and since a nomenclatorial transfer would add nothing to our regrettably small knowledge of it, I am not giving this obscure plant a new name under *Tournefortia*. However, I do strongly suspect that it belongs in that genus.

2. NOTES ON BRAND'S TREATMENT OF CRYPTANTHA

The treatment of *Cryptantha* by Brand appeared in the second and posthumous volume he contributed on the *Boraginaceae* in "Das Pflanzenreich." It is based almost exclusively upon the material available to him in the German herbaria. Having had no field experience in Western America and having had no opportunity to examine either the very numerous types or the great collections of *Cryptantha* in American herbaria, it is not surprising to find that Brand's treatment of the genus contains numerous errors arising from his restricted opportunities for

the study of this large, difficult and characteristic West American genus. I have found some of Brand's statements very puzzling. Hence it is that during a recent visit in Germany I took the opportunity of studying the material available to him and, in the light of these studies, made copious annotations in copies of his published work on the *Boraginaceae*. The data given here concern *Cryptantha* and embody the notes correcting Brand's more serious errors, as well as those clarifying the more puzzling details of his work on that genus. In the following discussion, as a heading for the pertinent notes, I have given the specific name accepted by Brand and have preceded it by the number under which the species may be found in his treatment. Following these is an abbreviated reference to the page of the *Pflanzenreich*, iv. 252² [Heft 97] pp. 28-75 (1931), on which the given species may be found.

5. *Cryptantha macrocalyx* (Phil.) Reiche; Brand, *Pflanzenr.* 30 (1931). — The specimen cited and described is evidently a duplicate of the material to be found in Philippi's Herbarium at Santiago labelled as collected by San Roman in Quebrada de Serna. The material is so poor that I can add nothing to my previous discussion, *Contr. Gray Herb.* 78: 70 (1927), of this peculiar plant. It is most certainly not *C. macrocalyx*.

6. *Cryptantha Buchtienii* Brand, *Pflanzenr.* 30 (1931). — I have studied the type-specimen. It is a form of *C. glomerata* from a locality in which it has been repeatedly collected.

7. *Cryptantha phacelioides* (Clos) Reiche; Brand, *Pflanzenr.* 31 (1931). — Brand cites two specimens as seen. The collection by Philippi, from which Brand's description is derived, is an isotype of *Eritrichium Rengifoanum* Phil., which I consider to be a phase of *C. aprica* (Phil.) Reiche. I have not seen the material collected by Buchtien, which is cited by Brand, but suspect that it may be *C. glomerulifera* (Phil.) Johnston, which Buchtien obtained at 2400 m. alt. near Juncal. Neither the name used by Brand nor any of the supposed synonyms he lists belong to either of these species I have mentioned. The synonyms he lists belong to three distinct species.

9. *Cryptantha talquina* (Phil.) Brand, *Pflanzenr.* 32 (1931). — This species is unquestionably a synonym of *C. alyssoides* (DC.) Reiche. Brand attempted to separate it by stating that basal cleistogenes were present in *C. talquina* and absent in *C. alyssoides*. This is contrary to fact. An isotype of *C. alyssoides* in the DeCandolle Herbarium at Geneva shows a fine display of these cleistogenes. The type at Paris has had them all knocked off.

12. **Cryptantha candelabrum** Brand, Pflanzenr. 33 (1931).—Based upon three collections, all from Philippi. These are: 1. Santiago, "*Philippi* (sub *E. congestum*), 2. Santiago, "*Philippi dedit 1876*" (sub *E. congestum*) and 3. Prov. de Santiago, "*Philippi dedit 1876*" (sub *E. lineare*; "*Dimorphocarpum est*"). The first specimen has flowers and fruit. The second and third show flowers only. For evident reasons the first specimen is selected as type. It is a form of *C. linearis* (Colla) Greene. The other specimens are quite similar and probably represent immature *C. linearis* or perhaps even *C. aprica*.

13. **Cryptantha fallax** (Phil.) Reiche; Brand, Pflanzenr. 33 (1931).—The specimen from Philippi, cited by Brand, seems to represent *C. Kingii* (Phil.) Reiche. The chasmogamic flowers are in bud only. The label associated with the specimen is in the script of Philippi. There is a question mark following the locality, "La Serena."

15. **Cryptantha campylotricha** Brand, Pflanzenr. 34 (1931).—This species is a synonym of *C. Kingii* (Phil.) Reiche.

16. **Cryptantha diffusa** (Phil.) Johnston; Brand, Pflanzenr. 34 (1931).—The single specimen cited, that collected by Philippi at Paihuano, represents *C. globulifera* (Clos) Reiche.

17. **Cryptantha modesta** Brand, Pflanzenr. 35 (1931).—This species is a synonym of *C. diplotricha* (Phil.) Reiche.

19. **Cryptantha Vidalii** (Phil.) Reiche; Brand, Pflanzenr. 35 (1931).—The only specimen examined by Brand is one grown in the Berlin Garden. It seems to be a form of *C. glomerata* Lehm. It is of course not authentic *C. Vidalii*.

21. **Cryptantha Candolleana** Brand, Pflanzenr. 36 (1931).—This species is based upon specimens from Macrae, Gay, Besser, and two from Philippi. At Berlin there is no specimen of this species collected by Gay in "Colchagua," but there is one given as from "Chile." All the material of this species cited by Brand represents forms of *C. glomerata* Lehm.

25. **Cryptantha globulifera** (Clos) Reiche; Brand, Pflanzenr. 37 (1931).—The only specimen cited by Brand seems to represent *C. linearis* (Colla) Greene. The specimen is immature. The corollas are evident.

28. **Cryptantha capituliflora** (Clos) Reiche, var. **compacta** Brand, Pflanzenr. 38 (1931).—The single specimen cited of this variety rep-

resents a stunted compact form of *C. diplotricha* (Phil.) Reiche. Brand does not appear to have seen any specimens of the true *C. capituliflora*.

33. **Cryptantha barbiger**a (Gray) Greene; Brand, Pflanzenr. 39 (1931).— Among the three specimens cited, those of Jones and of Heller represent this species. That collected by Greene represents typical *C. nevadensis* Nels. & Kenn.

34. **Cryptantha nevadensis** Nelson & Kennedy; Brand, Pflanzenr. 39 (1931).— The collection by Rusby, in the Dehra Dun Herbarium, which I examined while still on loan at Berlin, represents *C. barbiger*a (Gray) Greene.

38. **Cryptantha affinis** (Gray) Greene; Brand, Pflanzenr. 42 (1931).— The material at Berlin of *Heller 5882* is good *C. Torreyana* (Gray) Greene and that of *Jones 856* is at least in part good *C. affinis*. The data on the latter collection is probably questionable.

39. **Cryptantha microstachys** Greene; Brand, Pflanzenr. 42 (1931).— The single specimen cited by Brand, *Jones 3138* from San Diego, is *C. Clevelandi* Greene.

40. **Cryptantha Lyallii** Brand, Pflanzenr. 42 (1931).— This is a synonym of *C. flaccida* (Dougl.) Greene, all the cited material falling readily into that species.

49. **Cryptantha Hossei** Brand, Pflanzenr. 45 (1931).— This is an evident synonym of *C. diplotricha* (Ph.) Reiche.

63. **Cryptantha Famatinae** Brand, Pflanzenr. 49 (1931).— The type of this species represents *C. diffusa* (Phil.) Johnston.

66. **Cryptantha parvula** (Phil.) Brand, Pflanzenr. 50 (1931).— Of the three specimens cited, *Philippi 694* is *C. diffusa* (Phil.) Johnston, that from Caldera is a form of *C. globulifera* (Clos) Reiche, and that from San Roman is *C. diffusa*.

75. **Cryptantha leiocarpa** (Fisch. & Mey.) Greene, var. **eremocaryoides** Brand, Pflanzenr. 53 (1931).— This is apparently an odd form of *C. leiocarpa*.

81. **Cryptantha confusa** Rydberg; Brand, Pflanzenr. 56 (1931).— Among the specimens cited, *Leiberg 2271*, is *C. Watsoni* (Gray) Greene, the remainder represents *C. affinis* (Gray) Greene.

83. **Cryptantha Fendleri** (Gray) Greene; Brand, Pflanzenr. 57 (1931).— Greene's material from Beaver Creek is *C. ambigua* (Gray) Greene.

84. **Cryptantha Torreyana** (Gray) Greene, Brand, Pflanzenr. 57 (1931). — In the Berlin collections Rydberg & Bessey 4885 and Heller 9074 represent *C. ambigua* (Gray) Greene.

85. **Cryptantha Rattanii** Greene; Brand, Pflanzenr. 58 (1931). — The cited material at Berlin is in flower only. The corolla is 3–5 mm. broad. It is probably a form of *C. hispidissima* Greene.

86. **Cryptantha grandiflora** Rydberg, var. *anulata* Brand, Pflanzenr. 59 (1931). — This is a form of *C. Hendersoni* (Nels.) Piper.

91. **Cryptantha hispidula** Greene ex Brand, Pflanzenr. 60 (1931). — The type is *Baker 2966* from Napa County. The collections from Elmer and Eastwood are *C. Clevelandi* var. *florosa* Johnston.

91. **Cryptantha hispidula** var. **Elmeri** Brand, Pflanzenr. 60 (1931). — The cited material represents one of the forms of *C. Hendersoni* (Nels.) Piper having a single polished nutlet.

92. **Cryptantha flaccida** (Dougl.) Greene; Brand, Pflanzenr. 60 (1931). — The specimen collected by Congdon, no. 72, near Soledad represents *C. decipiens* var. *corollata* Johnston.

94. **Cryptantha hispida** (Phil.) Reiche; Brand, Pflanzenr. 61 (1931). — The cited specimen is an isotype of the very different *C. Romanii* Johnston.

96. **Cryptantha albida** (H. B. K.) Johnston; Brand, Pflanzenr. 63 (1931). — Among the cited specimens *Fendler 635* represents *C. Fendleri* (Gray) Greene, and the collection by Echegaray represents *C. diplo-tricha* (Phil.) Reiche.

106. **Cryptantha granulosa** (Ruiz & Pav.) Johnston; Brand, Pflanzenr. 65 (1931). — Two of the cited collections, *Weberbauer 5693* and *5700*, represent *C. limensis* (A. DC.) Johnston.

107. **Cryptantha Philippiana** Brand, Pflanzenr. 66 (1931). — This is a form of *C. glomerata* Lehm. having a developed chasmogamic inflorescence.

108. **Cryptantha mirabunda** Brand, Pflanzenr. 66 (1931). — I consider this species to be a synonym of *C. utahensis* (Gray) Greene.

113. **Cryptantha ambigua** (Gray) Greene, forma **robustior** Brand, Pflanzenr. 69 (1931). — The material cited from California all represents *C. echinella* Greene. One collection by Howell, no. 48, is *C. simulans* Greene.

115. *Cryptantha Stuebelii* Brand, Pflanzenr. 69 (1931).—The type of this species, from Yosemite Valley, is an equal mixture of *C. muricata* var. *Jonesii* (Gray) Johnston, and *C. simulans* Greene. Hansen's collection seems to be young *C. simulans*.

121. *Cryptantha Hansenii* Brand, Pflanzenr. 71 (1931).—This represents one of the puzzling forms of *C. intermedia* (Gray) Greene found in the foothills of the central Sierra Nevada. The variety *pulchella* Brand, is merely an immature specimen of this Sierran form.

3. NEW OR OTHERWISE NOTEWORTHY SPECIES

Cordia Weddellii sp. nov., arbuscula 3–4 m. alta laxe ramosa pilis malpighiaceis strigosa; ramulis pallide strigosis; foliis ellipticis 2.5–4 cm. longis 1.5–2.5 cm. latis utrinque strigosis, nervis 7–10-jugis rectis parallelibus inconspicue sparseque ramosis, subtus pallidioribus, margine integris, apice rotundis, petiolis gracilibus 5–9 mm. longis; floribus ad apicem ramulorum in cymulis parvis 3–10-floris breviter pedunculatis affixis; calyce ad anthesim ca. 1 mm. longo, apice irregulariter disrumpente, extus strigoso obscure multisulcato; corolla alba ca. 3 cm. longa extus pilosa intus glabra, tubo ca. 1 cm. longo 3–4 mm. crasso, faucibus late ampliatis, lobis 5 suborbiculatis ca. 1 cm. longis rotundis ascendentibus in alabastro valde plicatis; staminibus 5, supra (4 mm.) basem tubi affixis, filamentis inaequalibus 5 et 6 mm. longis glabris; antheris oblongis 2–2.5 mm. longis; stylo 4 mm. profunde lobato basim versus sparsissime setifero, lobis 1.5 mm. lobulatis, lobulis spathulatis; ovario glabro; fructu ignoto.

BOLIVIA: Prov. of Chiquitos, small shrub 3–4 m. tall at edge of forest, fl. white, Sept.-Oct. 1845, *Weddell 3454* (TYPE, Paris).

A very remarkable species of the section *Eucordia* and related to *C. aberrans* Johnston (*C. mucronata* Fres.) and *C. candida* Vell. These two relatives come from the Brazilian coast near Rio Janeiro. *Cordia Weddellii* was collected in the extreme eastern section of the Dept. of Santa Cruz, Bolivia, and is distinguished at once by its malpighiaceus hairs. This type of pubescence is extremely rare in *Cordia*. In the present species it is particularly interesting since the mid-section of each hair (above where it is attached) is glandular and thickened.

Cordia aberrans, nom nov. *Cordia mucronata* Fresenius in Martius, Fl. Bras. 8¹: 9 (1857); Johnston, Contr. Gray Herb. 92: 42 (1930); not Poiret (1818).

The existence of an earlier homonym makes it necessary to rename

this remarkable species. The type has been examined at Munich. It is labeled: "Inter Vittoria et Bahía; S. Princ. Maxim. Vidensis; Martius comunic. 1856."

Cordia taguahyensis Vellozo, Fl. Flum. 98 (1825) and Icones, 2: tab. 154 (1827). *Cordia amplifolia* Mez, Bot. Jahrb. 12: 538 (1890); Johnston, Contr. Gray Herb. 92: 62 (1930); not A. DeCandolle (1845). *Lithocardium Mezianum* Kuntze, Rev. Gen. 2: 976 (1891). *Cordia Meziana* (Kuntze) Gürke in Engler & Prantl, Nat. Pflanzenf. IV. Abt. 3a, p. 84 (1893).

An examination of the type of *C. amplifolia*, at Munich, proves it to be simply a very large-leaved northern form of *C. taguahyensis*. Blanchet has collected similar luxuriant forms in Bahía.

Cordia revoluta Hooker fil. Trans. Linn. Soc. London 20: 199 (1847); Riley, Kew Bull. 1925: 225 (1925). *Varronia revoluta* Hooker fil. ex Andersson, Kung. Svensk. Vet. Akad. Handl. 1853: 204 (1855); Andersson, Freg. Eugenies Resa, Bot. 84 (1861). *Lithocardium revoluta* (Hook. f.) Kuntze, Rev. Gen. 2: 977 (1891). *Sebestena revoluta* (Hook. f.) von Friesen, Bull. Soc. Bot. Genève, sér. 2, 24: 183 (1933). *Cordia linearis* Hooker fil., Trans. Linn. Soc. London 20: 199 (1847), not DeCandolle (1845). *Varronia linearis* Hooker fil. ex Andersson, Kung. Svensk. Vet. Akad. Handl. 1853: 204 (1855) and Freg. Eugenies Resa, Bot. 84, tab. 11, fig. 4 (1861). *Sebestena linearis* (Hook. f.) von Friesen, Bull. Soc. Bot. Genève sér. 2, 24: 182 (1933). *Lithocardium Hookerianum* Kuntze, Rev. Gen. 2: 976 (1891). *Cordia Hookerianum* (Kuntze) Gürke in Engler & Prantl, Nat. Pflanzenf. IV, Abt. 3a, p. 83 (1893).

GALAPAGOS ISLANDS: Narborough: Stewart 3177; Snodgrass & Heller 327. Albemarle: Snodgrass & Heller 28, 155, 196, 272, 897; Stewart 3169, 3170, 3172, 3173; Baur 213; Macrae (cotype of *C. revoluta*). James: Stewart 3175, 3176; Cheesman 388; Darwin (TYPE of *C. linearis*). Charles: Baur 214; Schimpff 215; Darwin (TYPE of *C. revoluta*).

I have had the opportunity of examining the types of *Cordia*, from the Galapagos Islands, described by Hooker and by Andersson. The study of this critical material, supplementing a careful examination of the large general collections from the islands preserved at the Gray Herbarium, has established specific identities which necessitate changes in the names currently applied to the island species. The above cited species and the three following are the only endemic species of *Cordia* on the islands. All belong to the section *Varronia*. While it may be generally stated that they are most closely related to the species of

western Peru and Ecuador, their immediate relationships on the continent are quite obscure. The three following species are closely related to one another but probably not immediately related to the well marked *C. revoluta*. The following key will aid in distinguishing the four insular endemics:

- Corolla elongate, tubular, length of tube 3-4 times the breadth of the weakly developed limb; leaves linear; stems and upper surfaces of the leaves covered with stout short appressed falcate hairs; inflorescence capitate *Cordia revoluta* Hook f.
- Corolla coarsely funnelform, length of tube less than 2 times width of the conspicuous spreading limb; leaves lanceolate; stems and upper surfaces of leaves with erect or ascending (at times minute) hairs; inflorescence tending to elongate; flowers short-stipitate at maturity.
- Upper surface of leaves with abundant minute stout forked hairs *Cordia Anderssoni* Gürke
- Upper surface of leaves with stiff slender spreading simple hairs.
- Stems and lower surface of leaves bearing a mixture of minute appressed forked or stellate hairs and coarser stiff erect simple hairs *Cordia Scouleri* Hook. f.
- Stems and lower surface of leaves with only stiff erect simple hairs *Cordia leucophlyctis* Hook, f.

Cordia Scouleri Hooker fil., Trans. Linn. Soc. London 20: 200 (1847). *Varronia Scouleri* Hooker fil. ex Andersson, Kungl. Svensk. Vet. Akad. Handl. 1853: 204 (1855) and Freg. Eugenies Resa, Bot. 83 (1861). *Lithocardium Scouleri* (Hook. f.) Kuntze, Rev. Gen. 2: 977 (1891).

GALAPAGOS ISLANDS: Albemarle: *Stewart* 3162. James: *Baur* 209; *Scouler* (TYPE). Indefatigable: *Svenson* 7.

This plant is particularly close to the two following. It appears to be rare. The few collections seen, other than the type, are all mis-determined as *C. galapagensis* or *C. leucophlyctis*. The mixed pubescence on the leaves and stems decisively separates it from those species.

Cordia Anderssoni (Kuntze) Gürke in Engler & Prantl, Nat. Pflanzenf. IV. Abt. 3a, p. 83 (1893). *Lithocardium Anderssonii* Kuntze, Rev. Gen. 2: 976 (1891). *Varronia canescens* Andersson, Kungl. Svensk. Vet. Akad. Handl. 1853: 203 (1855) and Freg. Eugenies Resa, Bot. 83, tab. 11, fig. 2 (1861), not *Cordia canescens* HBK. (1818).

GALAPAGOS ISLANDS: Albemarle: *Stewart* 3195. Abingdon: *Stewart* 3158. James: *Stewart* 3157. Duncan: *Baur* 215. Charles: *Lee*; *Andersson* (TYPE). Chatham: *Stewart* 3165, 3166; *Baur* 216; *Andersson* (det. *V. leucophlyctis*).

Cordia leucophlyctis Hooker fil. Trans. Linn. Soc. London **20**: 199 (1847). *Varronia leucophlyctis* Hooker fil. ex Andersson, Kungl. Svensk. Vet. Akad. Handl. **1853**: 203 (1855) and Freg. Eugenies Resa, Bot. 83 (1861). *Lithocardium leucophlyctis* (Hook. f.) Kuntze, Rev. Gen. **2**: 977 (1891). *Varronia scaberrima* Andersson, Kungl. Svensk. Vet. Akad. Handl. **1853**: 202 (1855) and Freg. Eugenies Resa, Bot. 82, tab. 11, fig. 3 (1861), not *Cordia scaberrima* HBK. (1818). *Lithocardium galapagosenum* Kuntze, Rev. Gen. **2**: 976 (1891). *Cordia galapagensis* (? Kuntze) Gürke in Engler & Prantl, Nat. Pflanzenf. IV. Abt. 3a, p. 83 (1893).

GALAPAGOS ISLANDS: Narborough; Snodgrass & Heller 331, 342. Albe-marle: Snodgrass & Heller 75, 136, 195, 291, 857, 881, 893; Stewart 3159; Baur 210, 212; Macrae; Darwin (TYPE of *C. leucophlyctis*). Indefatigable: Baur 211; Andersson (TYPE of *Varronia scaberrima*). Barrington: Stewart 3164. Hood: Stewart 3168.

The type of *C. leucophlyctis* and *Varronia scaberrima* are remarkably similar. The plant illustrated as *V. leucophlyctis* by Andersson, Freg. Eugenies Resa, Bot. tab. 11, fig. 1 (1861), appears to be *Cordia Anderssoni* from Chatham Island.

Cordia setigera, sp. nov., dumosa; ramulis gracilibus strigulosis; foliis lanceolatis 3–6.5 cm. longis 12–24 mm. latis tenuibus, apice acutis, basi cuneatis, margine evidenter irregulariterque arguto-dentatis, dentibus apiculatis, faciebus pilis numerosis 0.5–1 mm. longis ascendentibus asperatis (basibus pilorum saepe pustulatis) subtus pallidioribus, nerviis 4–6-jugatis perinconspicue pauceque ramosis, petiolis 1–5 mm. longis; pedunculis terminalibus gracillimis 1–7 cm. longis; inflorescentia congesto-capitatis 7–10 mm. diametro; corolla alba infundibuliformi 15–18 mm. longa, limbo ascendenti ca. 1 cm. diametro, lobis rotundis ca. 3 mm. longis; calycibus ad anthesim ca. 6 mm. longis sparse strigosis, tubo 2–2.5 mm. longo et crasso, lobis triangularibus ca. 1–1.5 mm. longis, apice linearibus 2–3 mm. longis attenuatis; fructu ca. 5 mm. longo apice exserto.

BRAZIL: near Fazenda de Bom Jardim, Rio Jequitinhonha, in north-eastern Minas Geraes, 1817, St. Hilaire B¹ 1478 (TYPE, Paris).

A very well marked species which keys out with *Cordia grandiflora* and *C. paucidentata* in my revision of the Brazilian species of *Cordia*, cf. Contr. Gray Herb. **92**: 20 (1930). From both of these species it is distinguished by its smaller corollas, its thin leaves, its sparsely setulose herbage, and its very sparsely strigose calyces. It is evidently a very slender loosely branched bush and hence quite different in habit from the much more southerly ranging *C. paucidentata*. *Cordia grandiflora*

has different pubescence, very much larger differently shaped corollas, and comes from the Amazon Valley. The closest relative of the proposed species is probably *C. Neowediana* DC., of the forests back of Ilhéos, Bahia. That species has more finely serrate, more hairy leaves, larger corollas, much larger brown-hairy calyces, and only short tips on the calyx-lobes. It is a plant of the wet coastal forests, *C. setigera* is a plant of the dry catingas inland.

Cordia Neowediana DeCandolle, Prodr. 9: 498 (1845); Fresenius in Martius, Fl. Bras. 8¹: 23 (1857), as *C. Neowidiana*; Johnston, Contr. Gray Herb. 92: 64 (1930). *Varronia macrocephala* sensu Nees & Martius, Nov. Acta Acad. Caes. Leop.-Carol. Nat. Cur. 11: 78 (1823). *Lithocardium Neowiedianum* (DC.) Kuntze, Rev. Gen. 2: 977 (1891).

The type of this species is preserved at Brussels. Through the kindness of Prof. W. Robyns I have had the privilege of borrowing it for study. The species is a well marked one and is certainly worthy of recognition. The single collection upon which it is based was obtained in southern Bahia, in the country back of Ilhéos. It is one of the species of the section *Varronia* having the flowers capitately congested. The large white corollas, in size and shape, are very suggestive of those found in the distantly related *C. paucidentata*. The stems, calyces and both leaf-surfaces are conspicuously bristly. There is no other kind of pubescence. The hairs are stiffish, spreading and mostly ca. 2 mm. long. Most of them spring from a small pustulate base. The hairs on the calyx are brown. The leaves are lanceolate, serrate and about 7 cm. long and 2 cm. broad. The calyx is ca. 1 cm. long, bristly, and sparsely glandular above the middle. The lobes are nearly 3 mm. long and triangular with a short subulate tip 1–1.5 mm. long. In my revision of the Brazilian species, l. c. p. 20, *C. Neowediana* keys out with *C. longifolia*, *C. poliophylla* and *C. leucocephala*, which are rather closely related to it. From these three species it can be quickly distinguished by its very bristly leaves and much larger bristly calyx.

Cordia Braceliniae, sp. nov., fruticosa diffusa; caulibus ca. 3 dm. longis laxe ramosis strigosis; foliis elliptico-obovatis vel oblanceolatis 2–3 cm. longis 10–17 mm. latis basim versus attenuatis, apice obtusis, margine crenatis, nervis 3–5-jugatis rectis ascendentibus vix ramosis supra impressis subtus prominentibus, facie laminae superiore sparse rigideque strigosis pilis pustulae insidentibus, facie inferiore pallidioribus strigosis vix pustulatis; pedunculis terminalibus gracilibus 2–3 cm. longis strigosis; inflorescentia capitata ca. 8 mm. diametro 20–25-flora; calycibus inflatis sparse strigosis ca. 3 mm. longis tubo pallido, lobis

triangularibus viridibus ca. 1.5 mm. longis breviter ca. 0.5 mm. longueque attenuatis; corolla alba 10–15 mm. longa; fructu irregulariter turbinato lacunoso vix exserto.

BRAZIL: Corinto beyond Retiro, Fazenda do Diamante, Minas Geraes, 590 m. alt., in thickety grassland, low spreading bush, fl. white and early deciduous, April 14, 1931, *Ynez Mexia 5617* (TYPE, Gray Herb.; isotype, Arn. Arb.).

A very distinct species perhaps most closely related to *C. paucidentata* of southern Brazil and adjacent regions. It is quickly separated from that species by its low branching habit, sparse strigose indument, and short-appendaged calyx-lobes. In my treatment of the Brazilian species of *Cordia*, Contr. Gray Herb. 92: 20 (1930), it keys out with *C. latifolia*, *C. poliophylla* and *C. leucocephala*, though it does not seem closely related to any of them. From these species, however, it is readily distinguished by its low spreading habit, small leaves lacking in secondary nervation, and different pubescence. The proposed species is strigose on the leaves, younger stems, peduncles and calyx. The hairs are abundant but do not cover the leaf-surfaces. They are stiff, straight and closely appressed. Those on the upper leaf-surface spring from small disks of dark mineralized cells. The type material has shrivelled corollas only. It has been distributed incorrectly determined as "*C. truncata*."

I find it a pleasure to associate with this well marked species the name of Mrs. H. P. Bracelin, of California. Her effective handling and distribution of the extensive collections of Mrs. Mexia make it fitting that her name should be associated with them and that it should be remembered by the students of the Brazilian flora.

Cordia campestris Warming, Kjoeb. Vidensk. Meddel. 1867: 12, fig. 2 (1868).

BRAZIL: Minas Geraes: Lagoa Santa, Pinhões, in campis, Jan. 28, 1866, *Warming* (Copenh., TYPE); Lagoa Santa, in campis ad Cabejeiras da lagoa, March 8, 1864, *Warming* (Copenh.); Formigas, *St. Hilaire sine no.* (Paris); indefinite, *Claussen 221* (G, K, Copenh., Stockh., Paris). Goyaz: Formosa, shrub, corolla white, Dec. 24, 1894, *Glaziov 21781* (K, BD, Paris).

Warming's species has been treated by me, Contr. Gray Herb. 92: 29 (1930), as a synonym of *C. multispicata* Cham. and several of the above collections cited under that species. *Cordia campestris* is very distinct from *C. multispicata*, however, and probably most closely related to *C. verbenacea* DC. and *C. chacoensis* Chodat, particularly to the latter. Among the Brazilian spicate species of the *Varronia* section, *C. multispicata* is readily recognized by having the pedunculate spikes prevail-

ingly lateral (and axillary) and the petiole of the subtending leaf evidently decurrent upon the peduncle, quite in the manner observable in *C. buddleyoides* Rusby, *C. axillaris* Johnston, and *C. guazumaefolia* (Desv.) R. & S. The specimens I have cited above, including the type of *C. campestris*, have terminal spikes and the petioles not decurrent on the peduncles. They are quickly separable from *C. verbenacea* by having the upper leaf-surface abundantly and evidently hairy. *Cordia campestris* is separated from *C. chacoensis* by its low habit of growth, and general coarseness of its parts. It appears to be a small (under 1 m. tall), sparsely branched shrub of the open country. The leaves are usually 3–5 cm. broad, and the spikes 5–10 cm. long. The flower buds are usually apiculate. It ranges in the campo of Minas Geraes and Goyaz. Its relative, *C. chacoensis*, ranges from southern-most Brazil into Paraguay and across northern Argentina.

Cordia guazumaefolia (Desv.) Roemer & Schultes, Syst. 4: 463 (1819). *Varronia guasumaefolia* Desvaux, Jour. de Bot. 1: 276 (1809). *Lithocardium guazumifolia* (Desv.) Kuntze, Rev. Gen. 3²: 206 (1898). *Cordia axillaris* var. *gymnocarpa* Johnston Contr. Gray Herb. 92: 35 (1930).

In my treatment of the Brazilian species of *Cordia*, l. c. p. 30, I cited *C. guazumaefolia* as a synonym of *C. corymbosa* (L.) Don. A recent study of Desvaux's type at Paris, however, has proved this to be quite incorrect. Among material from Jussieu's herbarium at Paris I have found specimens of this species determined by Desvaux. One of these is labeled, "Brasil, envoyé de Lisbonne pour M. Vandelli 1790." The plant described by Desvaux is evidently that which I treated as *C. axillaris* var. *gymnocarpa*. This plant should bear the name *C. guazumaefolia*. It may be added that while there is an evident relation between *C. axillaris* and true *C. guazumaefolia*, I am now of the opinion that their differences warrant specific rather than mere varietal separation.

Cordia insignis Chamisso, Linnaea 8: 122 (1833). *Cordia Haenkeana* Mez, Bot. Jahrb. 12: 560 (1890).

An examination of the type of *C. Haenkeana*, at Munich, makes it evident that it is only a form of *C. insignis*. The collection is given as having been collected by Haenke in Peru. The accuracy of this data, however, I greatly doubt. *Cordia insignis* is known only east and south of the Amazon Basin, from eastern Brazil to eastern Bolivia, and is certainly not to be expected in Peru.

Cordia laevior, sp. nov., arborescens, 6 m. alta; ramulis fusculis, juventate pilis brevibus adpressis vel ascendentibus vestitis mox glabrescentibus; foliis homomorphis oblongo-lanceolatis 15–26 cm. longis 4–10 cm. latis medium versus latioribus, basi acutis, apice longissime acuminatis, supra in costa et nervis primariis hirsutulis ceteris glabris, subtus pallidioribus, costa et nervis numerosis puberulentibus, nervis 7–8-jugatis, nervis tertiaribus obscuris, petiolis 5–10 mm. longis; cymis in furcis ramulorum ortis laxè ramosis; calyce in alabastro obovato 4–5 mm. longo 2.5–3 mm. crasso pilis minutis abundantibus vestito obscure costato, apice rotundo, lobis 5 plus minusve irregularibus triangularibus; corolla alba, tubo ca. 4 mm. longo, lobis ca. 2 mm. longis et latis, filamentis ca. 3 mm. longis basim versus pilosis; stylo sparse piloso; supra medium ovarii evidenter pilosis; fructu ignoto.

PERU: Pongo de Cainarachi, Rio Cainarachi, tributary of the Huallaga, dept. of San Martin, ca. alt. 230 m., tree 6 m. tall, fl. white, Sept.-Oct., 1932, *Klug* 2756 (TYPE, Arn. Arb.; isotype, Gray Herb.).

This species is related to *C. Sprucei* Mez, of the Rio Negro and the Guianas, from which it differs in having smoother, more elongate, less hairy leaves and a more loosely branched inflorescence. The leaves are not roughened above by slightly prominent repeatedly branched veinlets. The lower surface is much less hairy. The specimen was distributed as *C. Ulei* Johnston, from which, like *C. Sprucei*, it differs in having a very hairy ovary, finer pubescence on the lower leaf-surfaces, and more papery, more hairy, less regularly and sharply lobed calyces.

Cordia ripicola, sp. nov., arborescens 8–10 m. alta dichotome ramosa; ramulis sordidis pilis brevibus rigidulis scabridis; foliis subhomomorphis oblongis vel obovato-oblongis vel lanceolatis 8–14 cm. longis 3–7 cm. latis medio vel supra medium latioribus, apice acuminatis, basi acutis, supra sublucidis sparsissime breviterque strigosis, subtus minute rigideque hispidulis, nervis 6–8-jugis, nervis tertiaribus obscuris, petiolis 2–6 mm. longis; cymis gracilibus 3–10 cm. crassis laxè ramosis; calyce strigoso in alabastro obovato ca. 4 mm. longo 2–3 mm. crasso, intus supra medium strigoso, apice rotundo, ad anthesim in lobos 2–5 irregulares disrumpente; corolla alba 4–5 mm. longa, lobis ca. 2.5 mm. longis, filamentis ca. 3.5 mm. longis basim versus pilosis; ovario glabro vel summum ad apicem sparse pubescente; fructu ignoto.

PERU: Florida, Rio Putumayo, at mouth of Rio Zubineta, dept. Loreto, ca. 180 m. alt., "Chore-ey," forest along river, fl. white, tree 8–10 m. tall, May-June 1931, *Klug* 2262 (TYPE, Arn. Arb.; isotype, Gray Herb.) and 2277 (AA, GH).

A species related to *C. Sprucei* Mez and *C. laevior* Johnston, from

which it differs in having scattered appressed hairs on the upper face and abundant minute appressed ones on the lower face of the smaller, more oblong leaves. The calyx is more papery in texture and opens more irregularly. The style and ovary are sparsely hairy. The character of the calyx, the appressed hairs on the leaves and the hairiness of the pistil readily separate it from *C. Ulei* Johnston, the species under which the type has been distributed. *Cordia Ulei* comes from southwestern Brazil, at ca. lat. 11°S. The proposed species was collected nearly under the Equator. *Cordia ucayaliensis*, comb. nov. (*C. Ulei* var. *ucayaliensis* Johnston), readily distinguished by having the upper surface of the leaves strigose, comes from northeastern Peru.

Saccellium brasiliense, spec. nov., gracile; foliis lanceolatis 4–7.5 cm. longis 18–28 mm. latis medium versus latoribus, margine obscure sinuatis vel supra medium sparse denticulatis, supra viridibus pilos graciles rectos valde adpressos gerentibus, subtus pallidis distincte sericeis pilos abundantissimos minutos valde adpressos gerentibus, apice basique acutis, nervis 8–10-jugatis, petiolis 3–6 mm. longis strigosis; ramulis gracilibus laxe ramosis brunescensibus juventate sordide pubescentibus mox glabrescentibus, lenticellis numerosis orbiculatis pallidis punctatis; ramulis fertilibus 3–5 cm. longis ca. 5-foliatis; inflorescentia terminali paniculata 2–6 cm. longa folia vix superante; calycibus strigosis, dentibus laxe recurvatis.

BRAZIL: Corumba, Matto Grosso, Dec. 23, 1902, *Malme 2759* (TYPE, Herb. Berol.); Corumba, Dec. 22, 1902, *Robert 804* (BM, BD).

The two collections cited are devoid of corollas and are in early fruiting condition only. A study of the immature calyx and ovary, however, leave no doubt as to the generic relations of this interesting plant. The species is evidently a relative of the Bolivian *S. Oliveri*, but is readily separable by its small silky-strigose leaves and generally more compact habit of growth. *Saccellium brasiliense* has been reported from Corumba, doubtfully as *S. lanceolatum*, by Moore, Jour. Bot. 45: 405 (1907). Following I give the names of the known species of *Saccellium* and cite all the collections I have examined of these relatively rare species. The three known species may be separated as follows:

Plant glabrous or practically so; leaves 3–5 cm. broad, broadest at or slightly above the middle *S. Oliveri* Britt.

Plant evidently pubescent; leaves less than 3 cm. broad, broadest at or below the middle.

Leaves broadest near the middle, beneath silky strigose, lustrous, blade 4–7.5 cm. long; fertile branches 3–5 cm. long, bearing about 5 leaves; old branches brown, with evident pale lenticels *S. brasiliense* n. sp.

Leaves broadest near base, beneath velvety or somewhat tomentose, dull, blade 5–12 cm. long; fertile branches 10–20 cm. long, bearing about 10 leaves; old branches gray or only rarely brown, without evident lenticels....

.....*S. lanceolatum* H. & B.

Saccellium Oliverii Britton ex Rusby, Bull. Torr. Bot. Cl. 26: 147 (1899).

This species is known only from the type-collection made by Rusby, no. 2535, in May 1886 at 600 m. alt. at Guanai (or Huanay), Bolivia. The locality is in the department of La Paz at the confluence of the Rio Mapiri and Rio Tipuani at about lat. 15°30' S. and long. 68° W. in Amazonian Bolivia. Only fruiting specimens of the species are known. In its slender brownish branches, rather evident pale lenticels, and general leaf-outline, the species resembles *S. brasiliense* more than it does *S. lanceolatum*. The leaves are glabrous except for a few short inconspicuous ascending hairs along the midrib and principal veins. A similar scanty inconspicuous indument is also found in the inflorescence.

Saccellium lanceolatum Humboldt & Bonpland, Pl. Aequin. 1: 47, tab. 13 (1806); Humboldt, Bonpland & Kunth, Nov. Gen. 7: 209 (1825); Miers, Trans. Linn. Soc. London, Bot. 1: 25, tab. 6 (1875).

In two widely separated areas, 1. Northern Peru in northern parts (prov. Jaen) of the Dept. Cajamarca, lat. 5°–6° S., in the Amazonian drainage; 2. mountains of southern Bolivia (prov. Chuquisaca and Tarija) southward along the mountains of northern Argentina to Tucuman, ca. lat. 27° S.

PERU: between Jaen and Bellavista, prov. Jaen, 600–700 m. alt., shrub or small tree, common, April 29, 1912, *Weberbauer 6209a* (BD); Valley of the Marañon between Bellavista and the mouth of the Rio Chinchipe, prov. Jaen, 500 m. alt., small tree 4 m. tall, flowers white; accrescent calyces yellow-green, May 1, 1912, *Weberbauer 6226* (G, BD); Valley of the Marañon at the mouth of the Rio Chinchipe, prov. Jaen, 400–500 m. alt., tree 6 m. tall, flowers white, accrescent calyces yellowish green, April 30, 1912, *Weberbauer 6217* (G, BD); near Rio Huancabamba, *Bonpland* (TYPE, Paris; fragments, DC, Lindl., Gray). BOLIVIA: between Atajado and Parapiti, 700 m. alt., small tree, Dec. 1910, *Herzog 1192* (BD); south of Rio Pilcomayo, prov. Tarija, Feb. 18, 1916, *Steinbach 1776* (BD); Bolivia, Pampas, evergreen tree 4.5–6 m. tall, woods, May 1864, *Pearce* (BM). ARGENTINA: Isleta, Sierra Sta. Barbara, Jujuy, dry open place, tree 15–20 m. tall, July 5, 1901, *Fries 260* (Munich); Sierra Sta. Barbara, Salta, *Schuel 38* (G); Rio Blanco, dept. Oran, Salta, 650 m. alt., flowers yellowish, tree 10 m. tall, trunk 5 dm. thick, in high forest, Nov. 19, 1927, *Venturi 5546* (AA, G, K, BM); Abra Grande, dept. Oran, March 1927, 750 m. alt., tree 5 m. high, flowers yellowish, *Venturi 6780* (AA); Rio Piedras, dept. Oran, Nov. 15, 1911, *Rodriguez 85* (G); Campo Duran,

dept. Oran, a tree common on higher slopes, "Guayabil," Jan. 28, 1930, *Parodi 9269* (G); Tartagal, Salta, a tree, Feb. 1923, *Hauman* (G); hills near the crossing of the Rio Juramente, Salta, tree or shrub up to 6 m. tall, Feb. 21, 1873, *Hieronymus & Lorentz 295* (BD, Deles); Alemania, dept. Guachipas, Salta, 1100 m. alt., flowers white, tree 6 m. tall, in high forest, trunk 2 dm. thick, Dec. 22, 1929, *Venturi 10005* (G, K, BM); El Cadillal, dept. Burruyacu, Tucuman, Dec. 20, 1909, *Lillo 9823* (Deles); Tucuman, dept. Capital, alt. 450 m., tree 10 m. tall, flowers white, Dec. 12, 1907, *Lillo 7234* (G); Estate of Professor Lillo, dept. Capital, Tucuman, 460 m. alt., March 1925, *Venturi 3816* (AA); Tucuman, Dec. 12, 1907, *Stuckert 18375* (Deles); Tucuman, Feb. 10, 1910, *Lillo* (G).

The distinctly lanceolate leaves and the leafy, elongate stiffish branches readily characterize this species. The range of the tree is peculiar for it occurs in two far-separated regions in Peru and Argentina. Though this behavior suggests that two species or that a species and a variety is involved, a careful comparison of copious material has failed to produce any differences that would justify the proposal of even a new variety. The Peruvian plant differs from that of Argentina only in its perhaps somewhat sparser and slightly more slender pubescence on the herbage and in its somewhat darker stems.

In the *Plantae Aequinoctiales* 1: 47 (1806), the source of the original Humboldt & Bonpland collection of *Saccellium* is given as "ad rivos fluvii Guancabamba." Similar data are on the type-specimen at Paris. In the *Nova Genera*, 7: 208 (1825), the locality is given in more detail as follows: "inter Loxam et Tomependam Bracamorensium, ad ripas fluminis Guancabambae." The locality, Loja, of course, is in southern Ecuador. Tomependa is a ruined village near the junction of the Rio Chinchipe and the Rio Marañon. The Rio Huancabamba joins the Marañon about 50 km. above Tomependa. In all probability the type was collected in or near the province Jaen, in the region of northern Peru in which it has been collected by Weberbauer, *Bot. Jahrb.* 50: suppl. p. 92 (1914).

Coldenia conspicua, sp. nov., prostrata ut videtur annua; caulibus articulatis laxè ramosis 2–15 cm. longis, juventate dense graciliterque hispidulis et plus minusve glanduliferis; foliis aggregatis numerosis, lamina late lanceolata vel elliptica 5–13 mm. longa 2–5 mm. lata, subtus prominenter costata et nervosa (nervis 2–3-jugatis vix conspicuis) pilis gracilibus brevibus numerosis erectis asperata, supra pustulosa pilis robustioribus longioribus rigidioribus numerosis ascendentibus asperata, margine laxè revoluta integra vel obscurissime sparsissimeque crenata; petiolis gracilibus 2–9 mm. longis glanduliferis pilis abundantibus longis gracilibus erectis setosis; calyce 5-partito, lobis gracilibus basim versus

subinduratis et subnavicularibus praeterea linearibus hispidis glanduliferis ad anthesin ca. 9 mm. longis fructiferis ad 15 mm. longis; corolla conspicua coerulea, tubo ca. 9 mm. longo 2.5–3 mm. crasso lobis calycis subaequilongo intus glaberrimo, limbo 10–12 mm. lato patenti, lobis 4–5 mm. diametro, faucibus haud appendiculatis, filamentis 4–5 mm. longis glabris apicem versus tubi affixis ca. 2 mm. longe extrusis, antheris oblongis medio-affixis 1–1.4 mm. longis; stylo filiformi glabro 15 mm. longo 2 mm. profunde bilobato, stigmatibus 2 minutis obscure bilobulatis; nuculis 4 globosis 1.5–2 mm. diametro dense minuteque tessellato-tuberculatis per carunculas 1 mm. longas et crassas in apice receptaculi basaliter affixis; receptaculo ad anthesin cylindrico, fructifero turbinato.

PERU: sand flat near Mejia, Dept. Arequipa, 40 m. alt., flowers blue, Oct. 26, 1923, *Guenther & Buchtien 155* (TYPE, Inst. Bot. Hamburg); Mejia, July 21, 1923, *Guenther & Buchtien 156* (Hamburg); Mollendo, Dept. Arequipa, *Miss D. Stafford K60* (Kew).

A very distinct and remarkable species belonging to the Chilean and southern Peruvian section *Sphaerocarya*, Johnston, Contr. Gray Herb. 70: 57 (1924). The nutlets of the new species are quite similar to those of this section in size, shape and markings. From the previously described species of the section, however, *C. conspicua* differs in its extremely large corollas, its protruding stamens and its remarkable nutlet-attachment. The corollas are at least twice the size of those of any other species of *Coldenia*. The nutlet-attachment is also unique in the genus. In the known species of the section *Sphaerocarya* the immature nutlets are attached laterally at the middle of the sides of an erect subcylindrical gynobase. This is distorted somewhat by the crowding of the growing nutlets and tends to become constricted medially. After the nutlets have fallen away it is consequently more or less spool-shaped. In the proposed species the immature nutlets are borne laterally, not about the middle, but about the summit of the subcylindrical gynobase. By growth and the consequent pressure of crowding, the nutlets at maturity come to be attached basally in the expanded summit of the now turbinate gynobase. What is most peculiar is that each nutlet has a well developed strophiolate basal plug which is immersed in the gynobasal tissue. At maturity the strophioles loosen from the gynobase and with their attached nutlets fall away leaving 4 deep more or less united sockets in the much broadened apex of the gynobase. The mature gynobase, hence, becomes more or less cupulate.

The species is known only from along the coast in southern Peru in the general region of the port of Mollendo. The type has been reported, Bruns, Mitt. Inst. Allgem. Bot. Hamburg 8: 67 (1929), as *C. dicto-*

toma, but that species, of course, has small corollas and utterly different fruit-structures. The other species of the section *Sphaerocarya* are poorly understood. Since publishing, l. c., on the South American species of *Coldenia* I have seen the types of Philippi's species. I have been unable to separate his *C. litoralis*, *C. atacamensis* and *C. parviflora*, though from geographic considerations one would expect that the plant from the coastal region (*C. litoralis*) would be distinct from that of the high Puno de Atacama (*C. atacamensis* and *C. parviflora*). The type of *C. parviflora* is quite distinct from the Peruvian plants of the Arequipa region, which I cited under that name in my synopsis of the South American species of *Coldenia*. The correct name for this species is *C. elongata* Rusby! Its elongate leaf-blades, woolly petioles and calyces, and usually evidently crenate leaf-margins serve to distinguish it from Philippi's species. *Coldenia elongata* is known only from middle altitudes east of the coastal deserts of southern Peru and northern-most Chile. In Peru only two species of the section *Sphaerocarya* are known. These are *C. conspicua* which grows along the coast and *C. elongata* which grows along the cordilleras in the interior.

Coldenia Nuttallii Hooker, Kew Jour. Bot. 3: 296 (1851); Johnston, Contr. Gray Herb. 75: 43 (1925). *Coldenia decumbens* Hauman, Apuntes Hist. Nat. Buenos Aires 1: 55 (1909) and Anal. Soc. Cient. Argentina 86: 301 (1918).

This species so wide-spread in the intermontane area of the western United States has been known only from two small areas in the high cordilleras of Argentina, in northwestern San Juan, Johnston, Physis 9: 316 (1929), and in the Uspallata Pass region in Mendoza, Hauman, l. c. The plant was collected around 3000 m. alt. in San Juan and about 2300 m. alt. in Mendoza. A third locality for the species in South America, one much further south and so, not surprisingly, at lower altitudes, may now be put on record. I have seen a collection of *C. Nuttallii* in the herbarium at Munich which was obtained by Erik Ammann (no. 5) in Oct.-Nov. 1927, at 700 m. alt. near Cobunco, Neuquen, Argentina.

Tournefortia brasiliensis Poiret, Encyc. 5: 357 (1804); Johnston, Contr. Gray Herb. 92: 89 (1930).

I have studied the type of this doubtful species in the Lamarck Herbarium at Paris. It represents a specimen of *Vernonia scorpioides* (Lam.) Pers., with the flowers just beginning to develop. It is remarkably like, and probably a part of the collections by Commerson made at Rio Janeiro ("de l'île aux chats") in July, 1767. Consequently it may be a part of the same material as the type of *Conyza scorpioides* Lamarck, Encyc. 2: 88 (1790).

Heliotropium transalpinum Vellozo, Fl. Flum. 68 (1825) and Icones, 2: tab. 40 (1827). *Heliotropium tiaridioides* var. *schizocarpum* Johnston, Contr. Gray Herb. 81: 7 (1928), where other synonyms are cited.

Vellozo in describing and illustrating his species gave no indication as to whether the carpels were dorsally sulcate or not. Suspecting that the carpels were sulcate, however, since only plants with such developments were known about Rio Janeiro, I provisionally cited the name *H. transalpinum* among the synonyms of my *H. tiaridioides* var. *schizocarpum*. Vellozo's name, unhappily, is several years older than *H. tiaridioides* Cham., the species I then accepted. Subsequent study and consideration of much South American material of *Heliotropium*, not available when my monograph was written, has left no reasonable doubt as to the identity of the plant described and illustrated by Vellozo. The scores of specimens examined from São Paulo, Rio Janeiro, Minas Geraes and northward in Brazil, uniformly have sulcate nutlets, and there seems every reason for believing that Vellozo's plant had them also. I am accordingly taking up *H. transalpinum* as the correct appellation for the plant formerly treated by me as *H. tiaridioides* var. *schizocarpum*. The southern plant with non-sulcate nutlets, which I treated as *H. tiaridioides* var. *genuina* must have the new name I am publishing below. The type of *H. transalpinum* was collected in the state of Rio Janeiro near Boa Vista, ca. 9 km. up the Rio Parahyba from the town of Parahyba do Sul and beyond the coastal mountains (whence the specific name) from the city of Rio Janeiro.

Heliotropium transandinum var. *tiaridioides* (Cham.) comb. nov. *Heliotropium tiaridioides* Chamisso, Linnaea 4: 453 (1829). *Heliotropium tiaridioides* var. *genuina* Johnston, Contr. Gray Herb. 81: 6 (1928), where other synonyms are cited.

Heliotropium angiospermum Murray, Prodr. Stirp. Göttingen 217 (1770); Johnston, Contr. Gray Herb. 81: 10 (1928). *Heliotropium humile* Lamarck, Tab. Encyc. 1: 393 (1791).

In my treatment of the South American species of *Heliotropium*, Contr. Gray Herb. 81: 66 (1928), I cited *H. humile* Lam. as a doubtful synonym of *H. fruticosum* L. This I now find is incorrect. In the Lamarck Herbarium at Paris there is only one specimen determined by Lamarck as *H. humile*, this bears a label in his script reading: "heliotr. humile lam. illustr." The specimen is small but represents good *H. angiospermum*. The original description of Lamarck's species reads: "1757 HELIOTROPIUM humile. H. foliis ovato-lanceolatis villosis;

spicis solitariis lateralibus. Ex ins. Carib. Annum. *H. Dict. no. 6 Quoad descr.*" The reference is apparently to Lamarck's earlier account of *Heliotropium* in vol. 3 of the *Encyclopédie*, pp. 92-95 (1789), but no mention of *H. humile* is to be found there. Species no. 6 in the work is *H. fruticosum*, described as having linear-lanceolate leaves. Poiret, *Encyc. Suppl.* 3: 25 (1813), was evidently puzzled by Lamarck's description of *H. humile*. He mentions that species under *H. ternatum* but suggests that it might be *H. fruticosum*. I am content, however, to place *H. humile* among the synonyms of *H. angiospermum*, for the named specimen in Lamarck's herbarium seems authentic and agrees with the few words in the original description.

Lasiarrhenum pinetorum, sp. nov., herba; caulibus erectis simplicibus 10-15 cm. altis gracilibus strigosis foliosis; foliis lineari-subulatis 1-3 cm. longis 1-1.5 mm. latis sessilibus medio-costatis sed vix nervatis apicem versus caulis gradatim reductis margine valde revolutis supra sparse strigosis; floribus cymas terminalis 3-7-floris lineari-bracteatas aggregatis; pedicellis 2-3 mm. longis strictis strigosis; calycibus 5-lobatis ca. 4 mm. longis, lobis lineari-lanceolatis strigosis; corolla flava ca. 10 mm. longa extus strigosa, tubo ca. 4 mm. longo ca. 1.5 mm. crasso in fauces 3.5-4 mm. longas ca. 3 mm. crassas abrupte transmutato intus glaberrimo, lobis erectis oblongis 2.5 mm. longis 2 mm. latis apice rotundis; antheris glaberrimis 2 mm. longis oblongis basi sagittatis erectis (vix versatilibus) sub medium affixis; filamentis 4 mm. supra basim corollae affixis inclusis 1-1.3 mm. longis late alatis (in ambitu obovatis) apicem versus ca. 0.7 mm. latis; stylo 12 mm. longo filiformi longe (ca. 5 mm.) exsertis; fructu ignoto.

MEXICO: growing in the mountains in pine-forest, very rare, September, Ghiesbreght 311 (TYPE, Paris).

This is a remarkable species which is placed in *Lasiarrhenum* chiefly because of its broadly winged filaments. From *L. strigosum*, formerly the only known member of its genus, it differs in its very small size, its uninerved leaves, its glabrous anthers and its precociously long-exserted style. The rounded corolla-lobes and the expanded filaments separate *L. pinetorum* from the genus *Onosmodium*, while the long-exserted style, the erect corolla-lobes, the obovate filament and the sagittate anthers distinguish it from *Lithospermum*. No locality is given for this interesting plant. Ghiesbreght, however, collected chiefly in southern Mexico and mostly in the state of Oaxaca.

Lithospermum Muelleri, sp. nov., perenne; caulibus erectis gracilibus foliosis simplicibus vel rariter stricte et simpliciter longeque ramosis

2–5 dm. altis e radice crasso dense multicepitate rumpentibus strigosis vel basim versus breviter hispidis; foliis strictis firmis costatis sed vix nervatis vel rarissime perinconspicue sparseque nervatis, inferioribus oblongo-ellipticis, aliter lanceolatis, sessilibus, apicem versus caulis gradatim reductis 1–4 cm. longis 3–8 mm. latis, apice acutis, supra minute strigosis et pustulatis, subtus in margine et costa strigosis sed ceterum glabris; inflorescentia bracteata scorpioidea terminali solitari vel geminata vel ternata 3–10 cm. longa; calyce ad anthesin ca. 6 mm. longo, lobis inaequalibus cuneatis, pedicellis 1–3 mm. longis strigosis; corolla subcylindrica 15–19 mm. longa ca. 3 mm. crasso ut videtur flavescente intus glaberrima extus adpresse pubescente, lobis minutis ascendentibus suborbicularibus ca. 1 mm. diametro, faucibus inconspicue plicato-appendiculatis saepe plus minusve constrictis; staminibus 2 mm. sub apice tubi corollae affixis, filamentis ca. 1 mm. longis, antheris oblongis ca. 2 mm. longis inclusis; stylo filiformi ad anthesin 1–3 mm. longe extrusis; fructu ignoto.

MEXICO: common in pine belt above Mesa de la Camisa on the north slope of Sierra Tronconal between Cañon de los Charcos and Cañon de San Miguel, Sierra Madre Oriental, ca. 25 km. s. w. of Galeana, Nuevo Leon, 1800–2700 m. alt., June 4, 1934, C. H. & M. T. Mueller 739 (TYPE, Gray Herb.).

A very distinct species of uncertain affinities. Its subtubular corolla, frequently with a narrowly constricted ring about the throat, and its extremely small round ascending lobes, separate it from *L. strictum*, the only species I am inclined to believe which possibly may be a close relative of it.

Macromeria leontis, sp. nov., perennis erecta ca. 5 dm. alta e radice crasso profunde oriens; caulibus subsimplicibus pilis brevibus gracilibus erectis vel subretrorsis dense vestitis; foliis lanceolatis medium versus caulis grandioribus 4–10 cm. longis 1–2 cm. latis utroque acutis sessilibus evidenter nervatis, subtus pilis gracilibus brevibus erectis abundantibus vestitis vix pustulatis, supra viridis pustulatis et breviter hispidis; inflorescentia terminali evidenter bracteata; calyce 1.5–2 cm. longo, lobis linearibus, pedicello 1–5 mm. longo; corolla 5–7 cm. longo intus glaberrimo extus breviter pubescenti, tubo 2–3 cm. longo 1.5–2 mm. crasso supra in fauces 2 cm. longos 7–8 mm. latos gradatim ampliato, lobis triangularibus ca. 9 mm. longis et 6 mm. latis non rariter plus minusve recurvatis; antheris elongatis ca. 3.5 mm. longis; filamentis ca. 4 mm. infra apicem faucium corollae affixis 10–15 mm. longe exsertis; stylo filiformi tarde exsertis; fructu ignoto.

MEXICO: scattered in dense oak-woods on the ascent into Taray, Sierra

Madre Oriental, ca. 25 km. s. w. of Galeana, Nuevo Leon, ca. 2400 m. alt., June 5, 1934, C. H. & M. T. Mueller 754 (TYPE, Gray Herb.); scattered in dense pine and oak woods along the descent into Alamar, Sierra Madre Oriental, May 29, 1934, C. H. & M. T. Mueller 594 (G).

Probably a relative of *M. Pringlei*, but differing in having a fine slender spreading indument throughout. In *M. Pringlei* the more rigid, somewhat longer sparser hairs are closely appressed and the upper leaf-surfaces are a much clearer green than in *M. leontis*. The latter species has leaves noticeably grayer and duller in color.

Macromeria barbigera, sp. nov., perennis, setosa, robusta; caulibus erectis 5–8 dm. altis saepe simplicibus; foliis lanceolatis vel ovatis evidenter nervatis, inferioribus parvis vix persistentibus, ceteris latoribus 3–5 cm. latis 5–11 cm. longis subsessilibus basi plus minusve rotundis, superioribus elongatioribus et minoribus; floribus terminalibus in cymas racemosas bracteatas aggregatis; bracteis foliaceis 2–7 cm. longis 1–4 cm. latis; pedicellis ca. 5 mm. longis; calyce ad anthesin ca. 18 mm. longo, lobis inaequalibus subulato-linearibus erectis; corolla ut videtur flavescenti intus glaberrima 5–6 cm. longa recta vel plus minusve curvata, tubo 1.5–2 cm. longo 1.5–2 mm. crasso lobis calycis paulo longiore, faucibus e tubo abrupte ampliatis ca. 2 cm. longis 5–6 mm. crassis cylindraceis in alabastro paulo asymmetricis, limbo abrupte dilatato 12–15 mm. diametro, lobis 5–6 mm. longis acutis ascendentibus apicem versus recurvatis; filamentis in faucibus ca. 8 mm. infra sinibus loborum affixis inaequalibus 12–15 mm. longis glabris filiformibus exsertis; antheris oblongis medio-affixis; stylo filiformi breviter tardeque extruso; stigmato minimo bilobulato; fructu ignoto.

MEXICO: common in dense oak wood beyond the pine and fir belt, north slope of Sierra Tronconal between Cañon de San Miguel and Cañon de los Charcos, 1800–2700 m. alt., Sierra Madre Oriental about 25 km. s. w. of Galeana, Nuevo Leon, June 4, 1934, C. H. & M. T. Mueller 741 (TYPE, Gray Herb.).

Related to *M. Thurberi* but quickly separable by its more robust habit, larger broader leaves and very different pubescence. The foliage of *M. Thurberi* is copiously and finely strigose with an admixture of coarse more or less spreading hairs. In the proposed species the strigosity is lacking and the spreading hairs much longer and very conspicuous. The corollas of *M. Thurberi* have a much more abundant and paler indument than do those of *M. barbiger*a. The range of the new species is to the southeast of the most easterly station of its relative.

Evidently to be identified with *M. barbiger*a are collections made by Mueller in 1933. These specimens have been kindly sent to me from

the Field Museum by Mr. P. C. Standley. One of these collections, no. 174 from the "Trail to Puerto," Nuevo Leon, has leaves becoming 17 cm. long and 7 cm. broad. Its flowers are immature. The second collection, no. 173 from Diente Canyon, 21 km. south of Monterey, is evidently from a very mature plant and consists of the elongated inflorescence showing mature bracts and the old pedicels and calyces.

Among his collections of 1934 Mueller obtained one which may also represent a form of *M. barbiger*. This specimen, no. 830, was collected on Sierra Infernillo, about 25 km. s. e. of Galeana, Nuevo Leon, where it was common over small areas just below the crest, 2700–3000 m. alt. In leaf-outline and in general habit the plant suggests *M. Thurberi*, but differs in its lack of strigosity and in its very much less hairy flowers. The corollas differ from those of *M. barbiger*. They are somewhat smaller. The tube is gradually expanded towards the lobes and not abruptly expanded into a well developed cylindrical throat as I have indicated in my formal description above. In addition the corolla is slightly less hairy and the lobes not so acute. The plant is evidently related to *M. barbiger* and chiefly because of geographical considerations I am tentatively, at least, referring it to that species as a possible ecological form.

Havilandia opaca, sp. nov., procumbens; caulibus foliosis abundanter ascendenterque ramosis 1–1.5 mm. crassis in nodis radículas graciles gerentibus pilis brevibus rigidis appressis dense vestitis, internodiis 3–10 mm. longis; foliis firmis subcoriaceis costatis sed enervatis numerosis, apice rotundis vel obtusis, supra glaberrimis sparsissime pustulatis in costa sulcatis, subtus supra medium pustulatis in costa prominente strigosis ceteris glabris vel sparsissime strigosis, margine strigoso-ciliatis vel basim versus sparse ciliatis; foliis ramorum fertilium ellipticis 4–10 mm. longis 3–5 mm. latis, basi rotundis et oblique 1–2 mm. lateque sessilibus; foliis ramorum sterilium plus minusve oblanceolatis 8–12 mm. longis paullo sub apicem basim versus in petiolum 1 mm. latum ca. 2 mm. longum gradatim attenuatis; floribus solitariis numerosis axillaribus; corolla alba 4 mm. diametro, tubo ca. 1.2 mm. longo 1 mm. crasso intus glaberrimo, limbo patenti, lobis suborbicularibus ca. 1.5 mm. diametro, appendiculis faucium 5 intrusis trapeziformibus; antheris oblongis inclusis ca. 0.4 mm. longis, filamentis perbrevibus paullo supra medium tubi affixis; calyci ad anthesin 2 mm. longo, lobis 5 ciliatis latis, pedicello 0.5–1 mm. longo; nuculis 4 erectis angulate ovoideis 1 mm. longis opacis dense minutissimeque papillatis, dorso convexis, ventre angulatis, imam ad basim anguli ventralis ad gynobasim planum affixis.

BRITISH NEW GUINEA: common in open grassland, Murray Pass, Wharton Range, 2840 m. alt., prostrate herb forming masses 3 dm. broad or more, flowers white, June 12, 1933, *Brass* 4178 (TYPE, Gray Herb.; ISO-TYPE, NY).

A species evidently related to *H. papuana* Hemsl., from which it differs in its stout somewhat ovate, gray, dull, minutely papillate, rather than elongate, somewhat lance-lunate, black, lustrous, smooth nutlets. The margins of the leaves in *H. papuana* are evidently ciliate. In *H. opaca* the marginal hairs of the leaves, similar in size, number and position, are not spreading, but antrorsely appressed along the leaf-margin. The habit of growth in *H. papuana* is quite similar to that of *H. opaca*.

Havilandia robusta, sp. nov., procumbens; caulibus elongatis sparse ramosis; foliis coriaceis oblanceolatis 2–4.5 cm. longis 5–9 mm. latis paullo sub apicem basim versus in petiolum vaginatum gradatim attenuatis, apice rotundis vel subemarginatis, margine sparsissime strigosis, supra sparse strigosis, subtus glaberrimis vix nervosis, costa prominente sparsissime strigosa; floribus axillaribus; calycibus ad anthesin ca. 4 mm. longis, lobis lanceolatis margine sparsissime strigosis, pedicellis 5–7 mm. longis; calycibus maturitate ca. 6 mm. longis pedicellis 8–12 mm. longis; corolla 8–10 mm. diametro; nuculis 4 angulato-ovoideis opacis ca. 2 mm. longis dense minutissimeque papillatis, dorse convexis, ventre angulatis.

BRITISH NEW GUINEA: common about forest borders, Mt. Albert Edward, 3680 m. alt., June 1933, *Brass* 5681 (TYPE, N. Y. Bot. Gard.).

Evidently related to *H. opaca*, also of southeastern New Guinea, from which it differs only in being much larger in all its parts, and in having well developed pedicels and more elongate leaves. The upper surface of the leaves is lustrous and distinctly strigose.

Havilandia papuana Hemsley, Kew Bull. 1899: 107 (1899).

BRITISH NEW GUINEA: thickly massed on shallow soil over rock in grasslands, Mt. Albert Edward, 3680 m. alt., flowers white with yellow throat, June 18, 1933, *Brass* 4245 (G, NY).

This species was briefly, though adequately described by Hemsley from material obtained on Mt. Scratchley, 3660 m. alt., and in the Wharton Range, 3330 m. alt. It is known only from the high mountains of eastern British New Guinea.

The genus *Havilandia* is confined to high altitudes and consists of the three above enumerated species from British New Guinea, and *H. borneensis* Stapf from Mt. Kinabalu in British North Borneo. It is possible, in addition, that *Lithospermum minutum* Wernh., described from the Mt. Carstensz region in Dutch New Guinea, may also belong

to *Havilandia*. Unfortunately the type and only known collection of this puzzling species is so scanty and inadequate that it must remain an obscure, troublesome element in the flora of New Guinea until someone recollects it. The type consists of two minuscule snips in flower only, a ridiculously inadequate basis for the proposal of any species of Boraginaceae and certainly for one whose acquaintance with the genera of that family may be judged by his selection of the genus under which he essayed to publish the imperfect specimen from Dutch New Guinea.

Plagiobothrys Scouleri (H. & A.) Johnston, Contr. Gray Herb. 68: 75 (1923) and Contr. Arnold Arb. 3: 51 (1932). *Myosotis Scouleri* Hooker & Arnott, Bot. Beechey Voy. 370 (1840). *Allocarya media* Piper, Contr. U. S. Nat. Herb. 22: 107 (1920). *Plagiobothrys medius* (Piper) Johnston, Contr. Arnold Arb. 3: 58 (1932). *Allocarya divaricata* Piper, Contr. U. S. Nat. Herb. 22: 107 (1920).

The original and only mention of *Myosotis Scouleri* in the writings of Hooker & Arnott appears in the Botany of Capt. Beechey's Voyage in a note on a collection of *Plagiobothrys Chorisianus* from California. The note is as follows: "The flowers here are on pretty long pedicels, while the Columbia plant has them shortly pedicellate; the latter presents, besides, a different aspect, and may be called *M. Scouleri*; it appears very closely allied to *M. californica*, Fisch. et Meyer, but the corolla is longer than the calyx." Gray, who apparently never studied the type of *M. Scouleri*, applied the name to an erect-growing plant with geminate spikes of conspicuous corollas, which is widely distributed in western Oregon and Washington, and all subsequent writers have followed him in that identification. A study of the type, however, shows this usage to be quite incorrect.

The specimens evidently the type of *M. Scouleri* are to be found on a mixed sheet, formerly in the Hooker Herbarium, now at Kew. This sheet bears three different collections: (1) the specimen of *P. Chorisianus* mentioned in the Botany of Beechey's Voyage, (2) specimens of *P. scopulorum* (?) or *P. cognatus* (?) collected by Nuttall, and (3) three plants labeled: "N. W. Coast, Dr. Scouler." The latter evidently constitute the type of *Myosotis Scouleri* H. & A. Duplicates of this Scouler collection are to be found on a sheet from Bentham's herbarium, at Kew, labeled: "Am. bor. occ. Scouleri, 1828," and in the herbarium at Edinburgh labeled: "Columbia, Scouler, 1827, (932)." These collections appear to represent a form of the plant I have treated in my monograph as *Plagiobothrys medius* (Piper) Johnston. They have the rufous calyx-lobes, evident corollas, and the general habit of that species.

Scouler is known to have collected about the mouth of the Columbia and at many small ports along the coast of Washington and Vancouver Island. *Plagiobothrys medius* is the common species near the coast in northwestern Washington and on Vancouver Island, and there is every reason that Scouler should have encountered it. Though the nutlets of Scouler's collection show certain peculiarities not matched in the available material of *P. medius*, I believe that they can be accommodated in that concept. The nutlets of the type of *M. Scouleri* have the rather bony pericarp common in *P. medius*, but the ridge attending the lateral scar is very closely appressed to the latter and encloses an areole (entirely filled by the scar) scarcely, if at all, broader than long. The nutlets of *P. medius* are, however, very variable and I believe the nutlet-variations of *M. Scouleri* can be admitted without destroying the naturalness of the concept.

Plagiobothrys hirtus (Greene), comb. nov. *Allocarya hirta* Greene, Pittonia 1: 161 (1888). *Allocarya Scouleri* var. *hirta* (Greene) Nelson & Macbride, Bot. Gaz. 61: 36 (1916). *Plagiobothrys Scouleri* var. *hirtus* (Greene) Johnston, Contr. Arnold Arb. 3: 52 (1932). *Allocarya calycosa* Piper, Contr. U. S. Nat. Herb. 22: 101 (1920).

I have indicated above that the type of *Myosotis Scouleri* H. & A. has been misinterpreted. The earliest correct name for the plant that has been called *Krynitzkia*, *Allocarya* and *Plagiobothrys Scouleri* is *Allocarya hirta* Greene. It is, however, strictly applied only to a local plant of the Umpqua Valley, Oregon, which has evidently spreading rather than appressed pubescence. The common form of this species must bear the following name:

Plagiobothrys hirtus* var. *figuratus (Piper), comb. nov. *Allocarya figurata* Piper, Contr. U. S. Nat. Herb. 22: 101 (1920).

This strigose form ranging from Oregon to Vancouver Islands is common.

Plagiobothrys hirtus* var. *corallicarpus (Piper), comb. nov. *Allocarya corallicarpa* Piper, Proc. Biol. Soc. Wash. 37: 93 (1924). *Plagiobothrys Scouleri* var. *corallicarpus* (Piper) Johnston, Contr. Arnold Arb. 3: 52 (1932).

A local form of southern Oregon characterized by its deeply alveolate nutlets.

Plagiobothrys calandriniioides (Phil.) Johnston, Contr. Gray Herb. 78: 91 (1927). *Allocarya alternifolia* Brand in Fedde, Repert. 26: 169 (1929).

The type of Brand's species has been examined. The lowermost leaves are weathered and crowded and so account for the very misleading specific name. The plant is the common Patagonian *P. calandrinoides*.

Thaumatocaryon dasyanthum var. **Sellowianum** (Cham.), comb. nov. *Anchusa Sellowiana* Chamisso, Linnaea 8: 115 (1833). *Moritzia Sellowiana* (Cham.) Fresenius in Martius, Fl. Bras. 8¹: 63 (1857). *Thaumatocaryon Sellowianum* (Cham.) Johnston, Contr. Gray Herb. 70: 13 (1924) and 78: 16 (1927). *Moritzia dasyantha* var. *Sellowiana* (Cham.) Brand in Fedde, Repert. 27: 148 (1929).

This plant differs from typical *T. dasyantha* only in its smaller corollas and appressed pubescence. Difficulty with connecting forms has convinced me that Brand might best be followed in treating *Sellowianum* as a mere variety. A collection of this variety from the state of Rio Janeiro, by Glaziou (no. 8731), supplies the basis for Glaziou's astonishing report of *Cyphomattia lanata* in Brazil, Bull. Soc. Bot. France 57: Mém. 3: 480 (1910). I have examined the specimen at Paris so determined by Glaziou.

Hackelia patens (Nutt.), comb. nov. *Rochelia patens* Nuttall, Jour. Acad. Phila. 7: 44 (1834). *Lappula coerulescens* Rydberg, Mem. N. Y. Bot. Gard. 1: 328 (1900). *Lappula subdecumbens coerulescens* (Rydb.) Garrett, Fl. Wasatch Reg. 78 (1911). *Hackelia diffusa* var. *coerulescens* (Rydb.) Johnston, Contr. Gray Herb. 68: 48 (1923). *Hackelia coerulescens* (Rydb.) Brand, Pflanzenr. [Heft 97] IV. 252²: 130 (1931). *Hackelia Nelsonii* Brand in Fedde, Repert. 26: 170 (1929). *Lappula decumbens* Nels. ex Brand, Pflanzenr. [Heft 97] IV. 252²: 126 (1931), lapsus calami.

I have examined Nuttall's type of *Rochelia patens* at the British Museum. The specimen was collected "near the Flat-Head River" on June 8, 1833, by N. B. Wyeth. The specimen is a good one and is evidently conspecific with *Lappula coerulescens*, a species also based upon material from western Montana. The species is known from western Montana and Wyoming and westward into Idaho, northern Utah and northern Nevada.

Hackelia grisea (Woot. & Standl.), comb. nov. *Lappula grisea* Wooton & Standley, Contr. U. S. Nat. Herb. 16: 164 (1913).

A readily recognizable species of New Mexico and adjacent Texas. Its relatively small corollas, with ascending lobes, quickly distinguish it among the west American annual and biennial species of this genus.

Lappula echinata Gilibert, Fl. Lituanica, 1: 25 (1781). *Cryp-*

tantha Lappula Brand in Fedde, Repert. **24**: 56 (1928) and Pflanzenr. [Heft 97] IV. **252**²: 147 (1931).

In the Pflanzenreich Brand placed his *Cryptantha Lappula* among the synonyms of *Lappula Redowskii* (Hornem.) Greene. I believe, however, that the species belongs under *L. echinata* Gilib. The evident corollas and the gross aspect of the type are of that species. A microscopic study of the (immature) nutlets of *C. Lappula* seems to show a double row of lateral prickles. Finally the type is given as from Concepcion, Chile, a locality at which *L. Redowskii* is certainly not to be expected to grow naturally, though a busy port at which an aggressive weed, such as *L. echinata*, might be introduced without any cause for surprise.

Lappula echinata is generally accepted as introduced into North America. This seems probable, though it is to be noted that the plant was collected in the New World at a very early date. A specimen in the DuBois collection at Oxford is labeled "brot from Maryland by Mr. Wm. Vernon, 1698." Among Michaux's collections at Paris there is one of this species labeled as "Dans ville de Montreal, 1792." The Smith collections in London contain a specimen labeled: "North America, 1817, F. Booth." In the British Museum there is a collection made by Douglas, during 1826, "In the valleys of the Rocky Mts.," most likely in northeastern Washington. It seems to have been again collected in the latter region only within the past ten years, though it has been well known in the southern parts of western Canada for at least a generation. There are reasons to believe that the railroads may have much aided in the distribution north of the International Boundary. The plant has exhibited an evident, progressive increase and migration westward across the more northern of the western United States. It is now rapidly increasing in eastern Washington where it gives every evidence of being a recent immigrant.

Cryptantha circumscissa (H. & A.) Johnston, Contr. Gray Herb. **68**: 55 (1923).

A few years ago, l. c. **81**: 75 (1928), I reported this characteristic plant of western United States from near Zapala, Neuquen, Argentina. A second station in Neuquen may now be recorded. At Munich I have seen specimens labeled as collected by Erik Ammann (no. 7) at Cerro Mesa between Sept. and Nov. 1927. The new station is nearly 90 km. southeast of Zapala.

Cryptantha clandestina (Trev.), comb. nov. *Lithospermum clandestinum* Treviranus, Del. sem. a 1832 in hort. Bonnensi collect. p. 2 (1832-3). *Cryptantha glomerata* Lehmann, Del. Sem. Hamb. **1832**: 4 (1832), nomen nudum; Fischer & Meyer, Ind. Sem. Hort. Petrop. **2**: 8

and 35 (1836); Johnston, Contr. Gray Herb. 78: 58 (1927). *Cryptantha microcarpa* Fischer & Meyer, Ind. Sem. Hort. Petrop. 2: 8 and 35 (1836).

A study of the original description of *Lithospermum clandestinum*, and of old garden material representing it, has made it clear that it is that well known cleistogamic species of Chile, the two forms of which have passed as *Cryptantha glomerata* and *C. microcarpa*. Fischer & Meyer, when describing *C. microcarpa*, in fact, actually cited *L. clandestinum* as a synonym. In the Bonn seed-list for 1832, published in Dec. 1832 or Jan. 1833, the name *Lithospermum clandestinum* appears in the alphabetic list on the second of the pages of that quarto catalogue. A reference leads to a footnote which reads as follows: "Diffusum hispidum; fol. lanceolatis amplexicaulibus; calycibus subsessilibus ventricosis corollam excedentibus; seminn. granulatis. Annuum. Corolla alba, tubo ventricoso, limbo conniventi. Semina duo plerumque abortiunt. T[reviranus]." The name, *L. clandestinum*, appears again in the Bonn list for 1833, but not in those for 1834 or 1835.

Cryptantha glomerata Lehm. is the type-species of *Cryptantha*. Recently I had the privilege of consulting the extensive collections of old seed-catalogues at Berlin and Geneva. I now find it possible to record several important references in the history of that genus and species which were either unknown or unavailable to me at the time of my work on the group. The first mention of *Cryptantha glomerata* Lehm. and of the generic name appears in Lehmann's seed-list of the Hamburg Garden for the year 1832. The binomial appears as a mere name on page 4, thus: "*Cryptantha glomerata* Lehm." No description or explanation of the name is given! The list is dated 1832 and was probably published, as was customary with such lists, around the close of the year. No mention of the binomial is found in the Hamburg lists for 1830, 1831 or for 1833 or 1834. In 1835, p. 4, again without description, appears: "*Cryptantha glomerata* Lehm. (Del. Sem. 1832)." In 1836, p. 4, the following two names appear bare of description: "*Cryptantha glomerata* Lehm." and "*Cryptantha microcarpa* F. & M." These are repeated in the list for 1837, p. 4. In the list for 1838, p. 4, there is merely the name, "*Cryptantha microcarpa* F. & M." Fischer & Meyer, in their St. Petersburg seed-list for 1835, supplied the first descriptions of *Cryptantha glomerata* Lehm. and *C. microcarpa* F. & M. This Russian list bears a censor's date, Dec. 25, 1835, the equivalent of Jan. 5, 1836 of our present calendar. There is no mention of *Cryptantha* in the St. Petersburg list for 1834! Fischer & Meyer, when publishing and describing "*C. glomerata* Lehm." in their list for 1835, attribute the

name to "Bernhardi in litt." A study of Bernhardi's seed-lists, Sel. sem. hort. Erfurt., shows that the name "*C. glomerata* Lehm." appears as a mere binomial in those for 1833 (Jan. 18, 1834), 1834 (Feb. 24, 1835) and 1835. There is no mention of *Cryptantha* in the Erfurt list for 1832!

From the facts I have given it becomes evident that *Cryptantha glomerata* was in cultivation at Bonn and Hamburg in 1832. Treviranus immediately described the Bonn cultures as *Lithospermum clandestinum*. Lehmann applied to his Hamburg cultures the name *Cryptantha glomerata*, but did not describe it, that being done for him three years later by Fischer & Meyer who based their description on plants grown at St. Petersburg. There is no information as to the channels by which the species was introduced into cultivation. I suspect, however, that the original seed may have been obtained by Bertero, who collected the plant near the Rio Quillota, Chile, as early as 1828, and that seeds from this source may have been distributed from Turin.

Amsinckia intermedia Fischer & Meyer, Ind. Sem. Hort. Petrop. 2: 2 and 26 (1836).

This name appears bare in the alphabetic list on page 2 of the seed-list cited above. On page 26 (p. 1 of reprint) the following description is found, "A. INTERMEDIA. A. corolla fauce glabra nuda, limbo tubo subbreuiore; staminibus ad faucem insertis. — Corollae tubus $1\frac{1}{2}$ lin. longus, limbus fere 3 lin. in diametro, saturate aurantiacus maculisque 5 saturatioribus pictus. — Species intermedia *A. lycopsioidem* inter et *A. spectabilem*; a priore dignoscitur insertione staminum, a posteriore corollis longe minoribus et praesertim corollae tubo non (ut in illa) ad faucem plicis intrusis semiclausa. — Hab. cum sequente specie [*A. spectabilis*] circa coloniam ruthenorum Ross in portu Bodega Novae Californiae. Annua." The seed-list in which this description occurs bears the printed censor's date, Dec. 25, 1835. This equals Jan. 5, 1836 of the present calendar.

Through the kindness of Prof. B. A. Keller, Director of the Institute and Botanic Garden at Leningrad, I have received authentic material of *Amsinckia intermedia*. This consists of an authentic fragment of the species, from the herbarium of Meyer, one of the co-authors of the species, and a fine specimen from the plantings in the St. Petersburg Garden in 1836. The specimens agree with the interpretation of *A. intermedia* given by Suksdorf, Werdenda 1: 88 (1931). The plant is a member of that variable and bewildering island species that Macbride, Contr. Gray Herb. 49: 12 (1917), and Jepson, Man. Fl. Pl. Calif. 844 (1925), have incorrectly called "*A. Douglasiana*." Greene, Bot. S.

Francisco Bay, 262 (1894), and Jepson, Fl. W. Mid. Calif. ed. 2, 350 (1911), earlier treated it, partly as *A. intermedia* and partly as *A. spectabilis*. The name, *A. intermedia* F. & M., is properly applied to the polymorphous species which is common in California in the interior valleys and on hillsides back from the immediate vicinity of the ocean.

Amsinckia spectabilis Fischer & Meyer, Ind. Sem. Hort. Petrop. 2: 2 and 26 (1836).

This species appears on page 2 of the above publication as a bare name in an alphabetic list of seeds. On page 26 (p. 1 of reprint) the following description is found: "A. SPECTABILIS. A. corolla fauce glabra plicis intrusis semiclausula, limbo longitudine tubi; staminibus ad faucem insertis. Species pulchritudine florum insignis atque distinctissima. Corolla aurea, limbo 6 lin. in diametro, ad faucem plicis 5, squamulas simulantibus, aucta. Annua."

In 1925 through the kindness of Prof. Boris Fedtchenko, with the assistance of Miss Olga Enden, I received two generous fragments of authentic specimens of this species. The specimens were grown in the St. Petersburg botanic garden in 1835-36. They are given as grown from seeds collected at Fort Ross, California, by Wiedemann. These fragments were examined by Suksdorf, Werdenda 1: 96 (1931). He correctly identified them with the coastal plant that Brand, in Fedde's Repert. 20: 319 (1924), has described as *A. nigricans*. Brand's plant, Heller 5614, is from the type-locality of *A. spectabilis*. I have seen many specimens of this plant in various herbaria from numerous garden-cultures. While evidently conspecific, these specimens rarely have the corollas as well developed as that found in the original culture at St. Petersburg in 1835. This is not surprising. I have grown *Amsinckia* in a botanic garden and under glass and have in most cases discovered remarkable differences in habit of growth and corolla-size between my cultures and the wild specimen from which the seed was obtained.

Macbride, Contr. Gray Herb. 49: 7 (1917), in his monograph of the genus, has treated the coastal plant (the true *A. spectabilis* F. & M.) under the name "*A. intermedia*." Jepson, Man. Fl. Pl. Calif. 844 (1925), attempted to follow him and has described the coastal plant as "*A. intermedia*." His illustration, however, is the inland species, which just happens to be the true *A. intermedia* F. & M. Previous to Macbride's paper in the writings of Gray, of Greene, and of Jepson, the coastal plant appears as "*A. lycopsoides*." Macbride, l. c. 5, of course, was quite incorrect in applying the name "*A. spectabilis*" to the smooth-fruited *A. grandiflora* Kleeb ex Gray. The name *A. spectabilis* F. & M. properly

belongs to the strictly coastal plant of California that has small dark nutlets, acute more or less denticulate leaves, and a pair of the calyxlobes frequently more or less united. Abrams, Fl. Los Angeles, 335 (1904), seems to have been the only author who has properly applied the names *A. spectabilis* and *A. intermedia*.

***Amsinckia lycopsoides* Lehmann, Del. Sem. Hort. Hamburg 1831: 1 and 7 (1831).**

On the first page of the Hamburg seed-list for 1831 appears the name "*Amsinckia lycopsoides* Lehm."¹ The exponent refers to a note on page 7 where the following is found, "¹Genus novum e familia Borraginearum, praeter alias notas cotyledonibus 4 distinctissimum. Benthamia Lindl. in litteris (non Richard Monog. des Orchidees iles de France et de Bourbon pg. 43, t. 7, fig. 2)." In the seed-list for 1833, p. 3, and 1834, p. 3, the binomial appears perfectly bare. In 1835, p. 3, it is listed in company with *A. angustifolia* Lehm. In 1836, p. 3, and 1837, p. 3, it is listed as one of four species, *A. angustifolia*, *A. intermedia*, *A. lycopsoides* and *A. spectabilis*.

In the writings of Fischer & Meyer the binomial, *A. lycopsioides* Lehm., appears as a bare name in company of *A. angustifolia* Lehm., in the first St. Petersburg list, Ind. Sem. Hort. Petrop. 1: 2 (1835). In the next list, 2: 2 (Jan. 1836), it appears with *A. angustifolia*, *A. intermedia* and *A. spectabilis* and on page 26 (p. 1 of reprint) has the following note concerning it: "AMSINCKIA LYCOPSOIDES. A. corolla fauce barbata, limbo tubo triplo brevior; staminibus corollae tubo paulo supra basin insertis. — *A. lycopsioides* Lehm. delect. sem. h. Hamburg. 1831. — Tubus corollae 3½ lin. longus; limbus 2 lin. in diametro, vix latior."

The species, *Amsinckia lycopsoides* Lehmann, is the type of the genus *Amsinckia*. The Hamburg seed-list in which it was first published is dated 1831. That it was actually published that year is proved by the review of this publication in the Litteratur-Bericht zur Linnaea (vol. 6) which bears the title-page date of 1831. The description of the species, *Amsinckia lycopsoides* Lehm., by Fischer & Meyer, appears in a seed-list for the year 1835 but this pamphlet bears a printed censor's date, Dec. 25, 1835 which is the equivalent of Jan. 5, 1836 in our present calendar.

It is to be noted that when, in 1831, Lehmann published his generic name, *Amsinckia*, that he definitely associates it with *Benthamia* of Lindley. This latter generic name was published by Lindley, in the same year, but only as a nomen nudum, Lindley, Nat. Syst. 241 (1831).

It was undoubtedly based upon material collected by Douglas along the Columbia River. This is clearly indicated by specimens in herbaria at Cambridge, Kew, London and Geneva. In the Lindley Herbarium at Cambridge there is only one sheet that has been determined as *Benthamia* by Lindley. This contains Cuming's no. 512 from Valparaiso and a specimen labeled "North West Amer. H. H. G. 1827, Douglas." Lindley has written in the corner of the sheet "*Benthamia lycopsoides* Mihi." There are various strong reasons for believing that this sheet in Lindley's herbarium formerly bore only the material from Douglas and that the Cuming material was later added to it, probably after Lindley's annotation. At Kew there are two significant specimens. One from the Bentham Herbarium is labeled "*Benthamia lycopsoides* Lindl. M. S. sem. ex Amer. occid. ex Douglas, Hort. Soc. Hort. London, 6-6-28." A similar sheet from the Hooker Herbarium is labeled "*Anchusa*, fl. yellow, *Benthamia* Lindl. mss. N. W. Am. Douglas, cult." Lindley published only the genus name, *Benthamia*. The binomial "*Benthamia lycopsoides*" seems to have been published first by DeCandolle, Prodr. 10: 118 (1846). This reference is clearly based upon a specimen at Geneva bearing the following data: "*Benthamia lycopsoides* Lindl. ined., Hort. Sociét. horticult. in Chiswick 6 jun. 1828." The name on the label is in the script of Lindley. The source is written by DeCandolle. The date given is the same as that found on the sheet in Bentham's herbarium and falls within the period when A. DeCandolle visited London for work on his *Campanulaceae*. The herbarium of the Horticultural Society was sold to the British Museum. There is a specimen from this source at South Kensington labeled: "sandy plains of the Columbia, 1825 (according to Lindley a new genus)." Lindley was in charge of identifying the plants grown in the gardens of the Horticultural Society at Chiswick. All the specimens mentioned are probably from seeds grown at Chiswick. They all represent the plant recently described as *A. simplex* Suksdorf, Werdenda 1: 33 and 53 (1927 and 1931).

There are a number of good reasons for believing that Lehmann's genus *Amsinckia* and his species *A. lycopsoides* are based upon Lindley's genus *Benthamia* and *B. lycopsoides*. In the first place shortly before 1830 Lehmann travelled in England and met various botanists there. He was a well known student of the *Boraginaceae*. Lehmann, in any case, was later in correspondence with Lindley, for he cites his authority for *Benthamia* as "Lindl. in litteris," and we may well believe that he received seed or specimens of Douglas's curious borage from Lindley and grew it in the Hamburg garden. Lehmann devotes about half of his short description of *Amsinckia* to citing Lindley's unpub-

lished *Benthamia* and its earlier published homonym. The specific name used by Lehmann is that selected by Lindley. What is most important, however, is that an *Amsinckia* conspecific with Douglas's plant was in cultivation in various European botanic gardens under the name "*Amsinckia lycopsoides*." There is a specimen at Kew collected by J. Gay in the Jardin des Plantes at Paris in June 1833, only a year and a half after Lehmann published *Amsinckia*. This plant was grown under Lehmann's binomial and represents the species collected on the Columbia by Douglas. In conclusion it may be noted that the short descriptive notes concerning *A. lycopsoides*, given in 1835 by Fischer & Meyer, apply to the plant collected by Douglas.

A study of Douglas's Journal, p. 116 (1914), fortunately reveals some information as to the original source of *Amsinckia lycopsoides*. The plant is evidently that mentioned under the date of May 2, 1825, in an enumeration of collections made on "Menzie's Island, in the Columbia river, opposite the Hudson Bay Company's establishment at Point Vancouver." According to Piper, Contr. U. S. Nat. Herb. 11: 620 (1906), Menzie's Island is that now known as "Haydens Island." The notes by Douglas are as follows: "(151) *Myosotis* sp., annual; hirsute, branching; leaves long, entire; linear-lanceolate; flowers bright yellow; tube long; mouth of the corolla spreading, with a dark spot opposite teeth; seeds not yet known; this very interesting species was found on Menzie's Island in company with Mr. Scouler, who agreed with me to call it *Myosotis Hookeri* [not *Myosotis Hookeri* Clarke (1883)] after Dr. Hooker of Glasgow; scarce, only three specimens of it were found, two of which are in my possession. — I have since found it in abundance near all the Indian lodges above the Rapids of the Columbia. S[eed].". From these notes it is evident that seeds were not obtained on Menzie's Island and that, later, they were obtained somewhere above the Columbia Rapids. *Amsinckia simplex* Suksd. is known only from the general vicinity of Portland, Oregon (just south of Menzie's Island). It is scarcely separable from *A. arenaria* Suksd. which is reported from the Columbia Gorge and in eastern Washington. The name *Amsinckia lycopsoides* (Lindley) Lehmann is properly applicable to these concepts.

It has been shown that *Amsinckia lycopsoides* Lehm. is based eventually upon material collected by Douglas along the Columbia River. In subsequent paragraphs I have shown that *Lithospermum lycopsoides* Lehm. (1830) is based upon collections made by Scouler on the northwestern coast of Washington. In the writings of A. DeCandolle, Prodr. 10: 118, adnot. (1846), Gray, Synop. Fl. 2: 198 (1878), Macbride,

Contr. Gray Herb. 49: 7 (1917), Suksdorf, Werdenda 1: 101 (1931), etc., the binomial *Amsinckia lycopsoides* has been considered as merely a nomenclatorial transfer and as based upon *Lithospermum lycopsoides*. The similarity of the specific epithet is a mere coincidence. There are no reasons at all for supposing that these two species are identical. I have shown that *Amsinckia lycopsoides* is a plant from along the Columbia. *Lithospermum lycopsoides* is an earlier binomial, but since the specific name is preoccupied under *Amsinckia* it can not be legitimately transferred to that genus. A new name for the coastal plant of northwestern Washington is accordingly needed.

Lithospermum lycopsoides Lehmann, Pugil. 2: 28 (1830); Lehmann in Hooker, Fl. Bor. Am. 2: 89 (1838).

As was his custom in the Pugillus, Lehmann cited no specimens when he originally described *L. lycopsoides*. In the Flora Boreali-Americana, in which he contributed the *Boraginaceae*, however, he repeated his original description verbatim and cited the basic specimen. This latter is given as "Straits of de Fuca, N. W. America, Dr. Scouler." At Kew, from the herbarium of Hooker, there is a specimen that agrees perfectly with Lehmann's description and is labelled "*Lith. lycopsioides* Lehm. De Fuca, N. W. Am. Scouler." I agree with E. L. Greene, who has written on this sheet that "This, along with fragments in Herb. Benth. constitutes the type of *Lithospermum lycopsoides* Lehm. It has never been in cultivation." The plant is undoubtedly conspecific with that of northwestern Washington and adjacent Vancouver Island which has passed as "*Amsinckia lycopsoides*" in Piper's Flora of Washington, Contr. U. S. Nat. Herb. 11: 480 (1906), and in the monographs by Macbride, Contr. Gray Herb. 49: 7 (1917) and Suksdorf, Werdenda 1: 101 (1931). It is not the same species as *Amsinckia lycopsoides* Lehm., which is based upon specimens collected by Douglas near the Columbia. The present plant, a coastal species related to true *A. spectabilis* F. & M. of California, strangely has no synonyms. Since the specific name is preoccupied under *Amsinckia* a new name is needed. The plant may be called:

Amsinckia Scouleri, nom. nov. *Lithospermum lycopsoides* Lehmann, Pugil. 2: 28 (1830) not *A. lycopsoides* Lehmann (1831).

Amsinckia Douglasiana A. DeCandolle, Prodr. 10: 118 (1846).

I have examined the type of this species in the DeCandollean Herbarium at Geneva. It is clearly a species with tessellate nutlets and large showy corollas. I consider it conspecific with *A. Lemmonii* Mac-

bride, Contr. Gray Herb. 48: 50 (1916). Suksdorf, Werdenda, 1: 102 (1931), who has examined authentic material of *A. Douglasiana*, preserved at the Gray Herbarium, has considered it closely related to *A. Lemmonii* but separable from it. He places these two species together in his monograph. Gray erroneously cited the name *A. Douglasiana* in the synonymy of the common inland species of California. Not having seen the type of *A. Douglasiana*, Macbride, Contr. Gray Herb. 49: 12 (1917), was misled by Gray's erroneous citation and applied it to the common inland species of California. The plant treated as *A. Douglasiana* by Macbride, and by Jepson, Man. Fl. Pl. Calif. 844 (1925), who followed him, is properly identified as true *A. intermedia* F. & M. *Amsinckia Douglasiana* A. DC. is a relatively rare plant of the South Coast Ranges of California and was probably originally collected by Douglas in San Luis Obispo or southern Monterey counties during his journey from Monterey to Santa Barbara and return.

***Amsinckia parviflora* Bernhardt**, Selec. Sem. Hort. Erfurt. 1833: 1 and 4 (Jan. 1834).

On the first page of the Erfurt seed-list for 1833 two *Amsinckias* appear in the alphabetic list of names, *Amsinckia lycopsoides* Lehm. and *A. parviflora* Bernh. A reference to the last, fourth but unnumbered page of the seed-list gives the following note concerning *A. parviflora* Bernh.: "(1) *Lithospermum calycinum* Moris, cui cotyledones 4, s. potius 2 bipartitae, speciem *Amsinckiae* sistit, quam *A. parvifloram* vocarem. An *A. angustifolia* Lehm. eodem planta?" The list bears a printed date, Jan. 18, 1834. No species of *Amsinckia* are mentioned in the Erfurt seed-lists for the year 1832. *Amsinckia parviflora* Bernh. appears to be no more than a mere renaming of *Lithospermum calycinum* Moris. The two names are, accordingly, exact synonyms and apply to Bertero's plant from Rancagua, Chile, described and figured by Moris, Mem. Accad. Torino 37: 98 tab. 22 (1834). In 1834 Lehmann cited Bernhardt's binomial as a synonym of *A. angustifolia* Lehm. I am inclined to believe this is correct, for as I shall discuss, I suspect that Lehmann's species is also based upon Chilean material.

***Amsinckia angustifolia* Lehmann**, Del. Sem. Hort. Hamburg 1832: 3 (1832), nomen; Fischer & Meyer, Ind. Sem. Hort. Petrop. 2: 26 (1836), description.

The above binomial appeared as a bare name in the seed-list of the Hamburg garden for 1832. It appeared again as a bare name in the list for 1833, p. 3, was omitted in that for 1834, and in the list for 1835, p. 3, was cited as follows: "*Amsinckia angustifolia* Lehm. (*A. parvifolia*

Bernh. Sel. sem. h. Erf. 1833).” This reference was repeated in 1836, p. 3. In the list for 1837, p. 3, it again appears as a bare name.

In the first list from the garden at St. Petersburg, 1: 2 (1835) the name *Amsinckia angustifolia* also appears bare. In the next list from St. Petersburg, 2: 2 and 26 (1836), the name appears in the list of seeds and on page 26 (p. 1 of reprint) the following description and references are published: “A. ANGUSTIFOLIA. A. corolla fauce glabra nuda, limbo tubo duplo brevior; staminibus ad faucem insertis. *A. angustifolia* Lehm. delect. sem. h. Hamburg. 1832. *A. parviflora* Bernhardt select. sem. h. Erfurt. 1833. *Lithospermum calycinum* Moris. Enum. sem. h. r. bot. Taurinens. 1831 et in Mem. della Acad. d. Scienze di Torino Tom. XXXVII. p. 108. tab. XXII. — Corollae tubus vix 2 lin. longus, limbus vix 2 lin. in diametro. — A praecedente [*A. lycopsioides* Lehm.] floribus parvulis et praesertim staminum insertione diversissima.” All the references cited by Fischer & Meyer trace back to material, collected by Bertero in central Chile. What is more all the garden material, under the name *A. angustifolia*, seems best referred to the Chilean forms of the genus. All authors have applied *A. angustifolia* to the austral plant. There seems every reason for continuing to do so. I suspect that the cultures in European gardens were originally from seeds obtained by Bertero at Quillota or Rancagua, Chile, and subsequently distributed from Turin by Morris or Colla.

Omphalodes erecta, sp. nov., herba perennis erecta e caudice laxo ramoso oriens pilis mollibus gracillimis subcinerea; caulibus foliosis simplicibus vel supra medium sparsissime fertiliterque stricto-ramosis 3–6 dm. altis partibus maturis plus minusve glabrescentibus brunnescentibus 2–4 mm. crassis; foliis lanceolatis vel late lanceolatis 5–11 cm. longis 15–30 mm. latis (superioribus non-conspicue reductis) sub medium apicem versus in acuminem 1–3 mm. longam gracilem gradatim attenuatis, margine integerrimis basi angulatis vel subrotundis 3–6 mm. longe petiolatis, supra viridis sparse inconspicue pubescentibus non rariter minute pustulatis, subtus pallidis saepe pilis abundantibus longioribus subcinereis; inflorescentia gracili laxo racemosa simplice vel basaliter furcata ebracteata 5–15 cm. longa 0–1 cm. longe pedunculata; pedicellis ad anthesin 3–6 mm. longis ascendentibus, fructiferis ad 2 cm. longis saepe decurvatis vel subcontortis; calyx ad anthesin pallide denseque strigoso, lobis 5 inaequalibus lanceolatis ca. 4 mm. longis; corolla coerulea vel medium versus violacea, tubo ca. 3 mm. longo, appendiculis faueium 5 trapeziformibus ca. 1.3 mm. longis et latis apice subemarginatis, margine pubescentibus, limbo ca. 13 mm. diametro patente ultra

medium lobato, lobis 4-5 mm. longis rotundis, sinibus loborum inconspicue plicatulis; antheris oblongis inclusis medium versus bubo corollae affixis; filamentis perbrevis; stylo ad anthesin 2 mm. longo, fructifero conspicuis 9 mm. longo; stigmato disciformi; fructu 4-ovulato; nuculo solitario (3 abortis) minute appresseque strigoso depresso lateque ovoideo, (cum alis) ca. 8 mm. diametro, margine evidenter 1-1.3 mm. late alato, ala plana patenti leviter denticulata, dorso nuculae convexo.

MEXICO: common in dense oak-wood along an arroyo near Santa Ana, between Alamar and Taray, Sierra Madre Oriental, ca. 25 km. s. w. of Galeana, Nuevo Leon, corolla blue with a light violet center, July 3, 1934, C. H. & M. T. Mueller 992 (TYPE, Gray Herb.); scattered in fields and waste places in canyon above Alamar, Sierra Madre Oriental, 1500-1800 m. alt., June 2, 1934, C. H. & M. T. Mueller 680 (G).

A remarkable species differing from all its congeners in its coarse erect habit of growth. The general habit and appearance of the plant, indeed, is more suggestive of *Cynoglossum* than of *Omphalodes*. From the American species of its genus it is further distinguished by its large solitary nutlets which possess a weakly denticulate and spreading wing, rather than a strongly toothed upcurved one. The foliage of *O. erecta* is very distinctive. All the American species of the genus have long-petioled more or less cordate leaves. The new species has them very short-petioled and lanceolate. Only one Mexican species, *O. aliena*, has a similar bractless inflorescence. The plant is a remarkable addition to the list of Mexican Boraginaceae.

HERBARIUM, ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

LORANTHACEAE COLLECTED IN THE SOLOMON ISLANDS
BY L. J. BRASS AND S. F. KAJEWSKI, ON THE ARNOLD
ARBORETUM EXPEDITION, 1930-1932

B. H. DANSER

With plate 129

***Amylotheca* sp.**

San Cristóval Island: Waimamura, Brass 2849, Sept. 9, 1932, "common, parasitic on rain forest trees, stout shrub, branches smooth and glaucous, leaves very thick and fleshy, perianth of unopened flowers lower half pale red, upper greenish-yellow."

Indeterminable for lack of open flowers, but closely allied to *Amylotheca Versteegii* (Lauterb.) Danser from New Guinea and New Ireland, differing, however, by longer-pedicelled lateral flowers of the triads, more thickish inflorescences and flowers, obtuse bracts and more distinct calyx lobes.

***Dactylophora salomonica*, n. sp.**

Plate 129 a-b

Glabra, inflorescentiis floribusque iuventute forte parce tomentellis exceptis. Rami robusti; internodia foliifera teretia, iuventute apicem versus applanata nonnunquam ancipita, nodis dilatatis, postea teretia, 3-5 mm. crassa, nodis ad sesquiplo crassioribus. Folia opposita vel subopposita; petioli 14-24 mm. longi, basi teretes, laminam versus facie superiore profundius canaliculati; laminae triangulari-ovatae, plerumque 10-15 cm. longae, 5.5-7.5 cm. latae, basi rotundatae vel leviter cordatae, in petiolum contractae, apicem obtusum versus gradatim attenuatae, crassiusculae, fragiles, penninerves, costa facie inferiore basin versus magis prominente, costa cetera et nervis lateralibus primariis valde incurvatis utrinque distinctis paulum prominentibus. Inflorescentiae singulae in axillis foliorum et plures circum nodos defoliatos; pedunculi teretes, apice basique paulum incrassati, 15-20 mm. longi, 1-1.25 mm. crassi; axes ex internodiis 2 vel 1 compositi, quorum inferius 1-5 mm. longum, superius brevissimum; nodi deinceps circiter 8, 6, paucas triades ferentes; pedicelli triadum inferiores 8-10 mm. longi, c. 0.3 mm. crassi, superiores paucis mm. breviores; pedicelli florum lateralium 2-3 mm. longi; bractae bracteolaeque ovatae obtusae 1.25-1.5 mm. longae. Calycis tubus obovato-campanulatus, 3.5-4 mm. longus, 1.5-2 mm. latus, limbus brevissimus erectus vel nonnihil inflexus. Corolla statu

alabastri adulti 25 mm. longa, tertia parte inferiore inflata ad 3 mm. lata, tertia parte media gradatim ad 1 mm. attenuata, tertia parte superiore in clavam 6-angulam obtusam 1.5–2 mm. crassam incrassata, postea divisa in petala 6 sublinearia, a basi c. 1 mm. lata in duabus tertiis inferioribus gradatim ad 0.5 mm. angustata, in tertia parte superiore angustissime spathulata, apice acutiuscula crassiuscula, latere interiore c. 2 mm. supra basin squamula minima. Filamentorum pars libera c. 2 mm. longa; antherae c. 4 mm. longae, obtusae. Stylus a basi c. 0.6 mm. crassa gradatim angustatus, sub stigmatе c. 0.25 mm. crassus; stigma obovatum, styli apice vix crassius. Fructus obovato-ellipsoides, ad 9 mm. longi, 6 mm. crassi, superea collo solido 2 mm. longo et lato coronati, calycis rudimento vix ullo.

G u a d a l c a n a l I s l a n d : Vulolo, Tutuve Mt., 1200 m. alt., *Kajewski* 2497, April 14, 1931; "common, a loranthus growing on trees; there are two different coloured flowers, yellow and yellow pink, but there is no specific difference; fruit green when ripe, length 1.1 cm., diameter 6 mm., with a white flesh inside; fruit with a blunt point at end; the leaves are heated and rubbed on sore legs." — Vernacular name "Bitorchi."

The genus *Dactyliophora* was known, before now, only from New Guinea and New Ireland. *Dactyliophora salomonica* is closely allied to the New Guinea *D. verticillata* (Scheffer) Van Tieghem, and perhaps only a variety of it, but it differs by less cordate, longer-petioled leaves, axillary inflorescences, longer and less thick peduncles and pedicels, more slender calyces and shorter corollas. The peculiar beak on the fruit is not described for any other species, but as in most *Dactyliophorae* the fruit are unknown, and those of *D. Novae-Guineae* (Bailey) Danser are figured with a similar prolongation (cfr. Bull. Jard. Bot. Buitenz., sér. 3, 11: 359, fig. 14, h), it probably is not a characteristic of *D. salomonica* only.

Sogerianthe versicolor, n. sp.

Plate 129c-e

Omnis glabra (vel pedicellis, bracteis, calycibusque minute puberulis). Rami graciles, parce dichotome ramosi, internodiis foliiferis 1–2.5 (–3) mm. crassis, plerumque 3–9 cm. longis, nodis valde incrassatis, duplo vel fere triplo crassioribus. Folia opposita; petioli 5–10 mm. longi, supra applanati praesertim laminam versus, subtus rotundati; laminae oblongo-ovatae, plerumque 6–10 cm. longae, 2.5–4.5 cm. latae, sub basi rotundata in petiolum contractae vel magis attenuatae, apicem obtusum versus magis minusve acuminatae, crassiusculae, fragiles, utrinque opacae (vel facie superiore lucidulae), penninerves, costa facie inferiore prope basin valde prominente, ceterum costa nervisque lateralibus primariis incurva-

tis utraque facie visibilibus vix prominentibus. Flores singuli vel in umbellis paucifloris omnino sessilibus in scrobiculis corticis inserti, pauci in axillis foliorum vel plures circum nodos foliatis et defoliatis; pedicelli teretes, basi saepe paulum clavati, 2–4 mm. longi, 0.3(–0.5) mm. crassi; bractee bracteolaeque triangulares vel ovatae, 0.5–1 mm. plerumque 0.75 mm. longae, obtusae vel acutae, basi nonnihil connatae. Calycis tubus campanulatus, subcylindricus, (1.5–)2–2.5 mm. longus, 1.25 mm. latus, limbus erectus paulum cupuliformis, 1(–1.25) mm. longus, ore (1.75–)2 mm. lato, integerrimus (vel irregulariter incisus). Corolla sympetala, statu alabastri adulti (24–)30–31 mm. longa, in duabus tertiis inferioribus fusiformiter inflata ad 3 mm. lata, in tertia parte superiore subcylindrica, c. 1.5 mm. lata, apice obtusa, postea divisa usque ad dimidiam longitudinem in lacinias 6 lineares reflexas et volutas apice crassiusculas acutiusculas, facie interiore prope basin squamulis nullis. Filamentorum pars libera 3.5–4 mm. longa; anthera basifixae, 3.5 mm. longa, obtusa. Stylus corollae aequilongus (vel paulo longior), a basi ad apicem aequicrassus; stigma globosum, styli apice circiter sesquiplo crassius. Fructus ellipsoides, ad 8 mm. longus, 4 mm. diametro, calyce integro erecto paulum aucto coronatus.

San Cristóval Island: Waimamura, lowlands, on rain forest trees, *Brass* 2676 (type), Aug. 18, 1932, "plentiful, leaves very pale, corolla-tube white, segments pink, filaments pink, style green."

Malaita Island: Quoimonapu, 200 m. alt., rain forest, *Kajewski* 2355, Dec. 12, 1930, "common, a large loranthus growing on the rain forest trees, base of corolla pink, ends of petals white cream."

Ysabel Island: Tiratona, 600 m. alt., *Brass* 3227, Nov. 26, 1932, "common, leaves stiff, margins incurved; perianth reddish, with brown lobes." — Vernacular names "Oong" (under no. 2355), and "Buraronu" (under no. 3227).

Description after the type *Brass* 2676, the dimensions between brackets after *Kajewski* 2355, which mainly differs by shorter corollas 24–26 mm. long, and puberulous pedicels, bracts and calyces. The number *Brass* 3227 is much like the type, but the leaves are much smaller, including the petioles 2–5.5 cm. long and 1–1.6 cm. broad.

The new species does not show the articulation in the pedicel nor the scales at the inside of the corolla tube considered characteristic for the genus *Sogerianthe* till now. As, however, it has a 6-merous long-tubed sympetalous corolla and 3 bracts at the base of the flower, and moreover agrees with the species already known in general appearance, I do not hesitate to place it in the same genus with *S. sogerensis* (S. Moore) Danser and *S. sessiliflora* Danser.



DACTYLIOPHORA SALOMONICA Danser (a-b)
SOGERIANTHE VERSICOLOR Danser (c-e)

Dendrophthoe falcata (Linn. fil.) Ettingshausen in Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Cl. **32**: 53 (1872). — Danser in Bull. Jard. Bot. Buitenz. sér. 3, **11**: 403 (1931).

Loranthus falcatus Linn. fil., Suppl. 211 (1781).

G u a d a l c a n a l I s l a n d: Berande River, sea level, *Kajewski* 2415, Jan. 6, 1931, "common, a loranthus growing on rain forest trees, petals green-cream with orange edges, very showy, the largest fruit on specimens, the natives say are pretty full growth, length 1 cm., diameter 4 mm.; the natives use this plant superstitiously to stop rain by placing twigs upright in the ground." — Vernacular name "Ti-nu-issi."

D i s t r i b u t i o n: from tropical southeastern Asia all over the Malay Archipelago to tropical Australia, but before now not collected farther eastward than the Bismarck Archipelago.

For the very numerous synonyms cfr. Verh. Kon. Akad. Wetensch. Amsterdam, Afd. Natuurk., sect. 2, **29**, 6: 44 (1933).

Notothixos leiophyllus K. Schumann in Schumann & Lauterbach, Nachtr. Fl. Deutsch. Schutzgeb. Südsee, 260 (1905). — Danser in Bull. Jard. Bot. Buitenzorg, sér. 3, **11**: 456 (1931).

Y s a b e l I s l a n d: Tataba, 50 m. alt., parasitic on branches of tall rain forest trees, *Brass* 3432, Jan. 4, 1933; "plentiful, small much branched shrub, leaves brittle, underside glaucous in old leaves, indumentum golden yellow."

D i s t r i b u t i o n: Philippine Islands, eastern part of the Malay Archipelago, Queensland, but before now not farther eastward than New Britain.

EXPLANATION OF PLATE 129

Fig. a and b: *Dactylophora salomonica* (type, *Kajewski* 2497); a, twig with leaves and inflorescences in bud, $\times \frac{1}{2}$; b, fruit, $\times 1$. Fig. c-e: *Sogerianthe versicolor* (type, *Brass* 2676); c, twig with flowers in bud, $\times \frac{1}{2}$; d, flower, $\times 1$; e, fruit, $\times 1$.

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CHROMOSOME NUMBERS IN THE HAMAMELIDACEAE AND THEIR PHYLOGENETIC SIGNIFICANCE

EDGAR ANDERSON AND KARL SAX

With three text figures

REINSCH¹ introduced his morphological survey of the Hamamelidaceae by the observation that they form one of those natural families as to whose precise delimitation and relationships there has been much difference of opinion. The forty years which have elapsed since the appearance of his paper have merely provided further illustrations of the justice of his remarks. Though universally conceded to be a natural group, the only general agreement as to its phylogenetic position seems to be the opinion that it occupies an important one. Because of this uniformly recognized phylogenetic significance an effort has been made to make as complete a survey of chromosome numbers as possible. The living collections of the Arnold Arboretum fortunately include several genera such as *Sinowilsonia* and *Parrotiopsis* which are very rare in cultivation but the work has been hindered by the very great technical difficulties involved. The chromosomes are small, there is much secondary pairing, the cytoplasm is murky and the chromosomes do not stain sharply. In most of these details the family shows cytologically a strong resemblance to the Rosaceae, paralleling the morphological resemblances which have been commented on by most students of the group.

The following chromosome counts have been made. The genera are arranged according to the classification of Harms in Engler and Prantl. In each case the counts were obtained from aceto-carminic smears. Typical meiotic plates are illustrated in Figure 1.

SUB-FAMILY HAMAMELIDOIDEAE		CHROMOSOME NUMBER
Tribe 1	<i>Hamamelis vernalis</i>	12
Tribe 3	<i>Corylopsis pauciflora</i>	12
	<i>Corylopsis spicata</i>	36
	<i>Corylopsis Veitchiana</i>	36
Tribe 4	<i>Parrotiopsis Jacquemontiana</i>	12
	<i>Fothergilla major</i>	36
	<i>Fothergilla monticola</i>	24
Tribe 5	<i>Sinowilsonia Henryi</i>	12
SUB-FAMILY LIQUIDAMBAROIDEAE		
	<i>Liquidambar styraciflua</i>	15

¹Engler in Bot. Jahrb. 11: 347 (1890).

Meiotic irregularities, accompanied by a high percentage of pollen sterility were encountered in *Liquidambar Styraciflua*. This is somewhat puzzling since this species exhibits none of the morphological peculiarities which are usually associated with irregular meioses. It is a "good" species with no closely related forms occurring within the same area. Its behavior is more probably to be explained as due to climatic influences. It is a southern species and at the Arboretum is being culti-

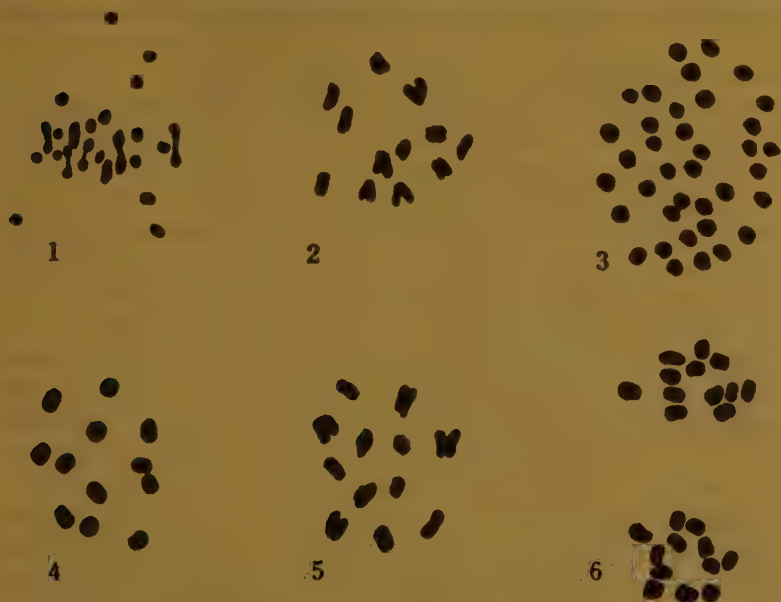


FIGURE 1. Camera lucida drawings ($\times 3000$) of pollen mother cells: 1. *Liquidambar Styraciflua*. — 2. *Parrotiopsis Jacquemontiana*. — 3. *Fothergilla major*. — 4. *Corylopsis pauciflora*. — 5. *Sinowilsonia Henryi*. — 6. *Hamamelis vernalis*.

vated somewhat north of its natural range. Whitaker¹ has demonstrated the effect of abnormal temperatures upon meiosis in *Cyphomandra*. It is possible that the irregular chromosome behavior and consequent pollen sterility of *Liquidambar Styraciflua* at the Arnold Arboretum may have a similar explanation. It would be interesting to know if *L. Styraciflua* is characterized by low percentages of fertile pollen in its native home.

The cytological studies present a number of facts of taxonomic significance. 1. The Hamamelidoideae are a coherent group with a com-

¹Jour. Arnold Arb. 15: 113-117 (1933).

mon base number. 2. The count on *Liquidambar* suggests that the Liquidambaroideae may possibly be derived from a different stock than the Hamamelidoideae since they apparently have a different base chromosome number. If this difference in base number should be found to persist in the other genus of that sub-family it would indicate that the divergence between the two sub-families occurred before the differentiation of the family as a whole. This is in accordance with the views expressed by Harms.¹ Summarizing the anatomical evidence he states² that the Hamamelidoideae are a unified group anatomically while the other subfamilies, particularly the Liquidambaroideae, have many distinctive peculiarities. Reviewing the entire evidence of relationship³ he suggests that the Liquidambaroideae are so distinctive that they might well be considered a separate family.

3. Polyploid series have been found in *Fothergilla* and *Corylopsis* and are not to be unexpected in other genera of the family when these are investigated more extensively. This discovery is of some taxonomic consequence since it indicates that in such genera we may expect phylogenetic relationships between species which will be, in part at least, reticulate. That is to say that a complete phylogenetic tree of the genus *Fothergilla* or *Corylopsis* would show anastomosing branches. It will be noted that *Fothergilla monticola* has 24 pairs of chromosomes and is therefore a tetraploid and that *F. major* with 36 pairs is a hexaploid. The phylogenetic relationships within and between these two species, as indicated by these chromosome counts, must be intricate. These two species are so similar that it is very doubtful if *F. monticola* deserves more than varietal rank.⁴ The cytological evidence would suggest that *F. monticola* is merely a tetraploid variety which arose spontaneously from the hexaploid species *F. major*. Such relationships are not unknown in other genera of the flowering plants. Erlanson for instance has shown⁵ that *Rosa acicularis* var. *Sayi* (Schw.) Rehder is an octoploid race ($2n = 56$) of the hexaploid species *Rosa acicularis* ($2n = 42$).

To the larger problem of the phylogenetic position of the family itself this cytological survey contributes important evidence, though unfortunately not as decisive as the obscurity of the case requires. Before going into details it may be said that on the whole the cytological evidence favors Hutchinson's interpretation of the phylogenetic position of

¹Engler Prantl Nat. Pflanzenf. 2. Aufl. 18a: 303-345 (1930).

²loc. cit. p. 307.

³loc. cit. p. 316.

⁴Anderson in Arnold Arb. Bull. Pop. Inform. ser. IV, 1: 61-64 (1933).

⁵Bot. Gaz. 96: p. 231 (1935).

the Hamamelidaceae.¹ Comparisons of two treatments of the family are presented in Figure 2. The numbers in the diagram are the base chromosome numbers so far as they have been determined.^{2 3}

By inference and by actual experimental test two kinds of change of chromosome number have been established as occurring in the higher plants; (1) the addition of whole sets of chromosomes, that is of two

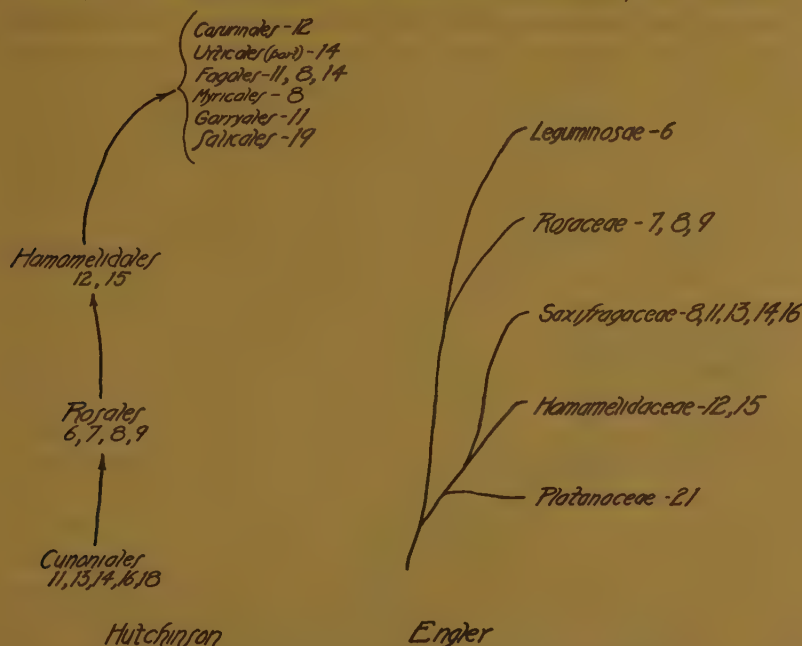


FIGURE 2. The phylogenetic position of the Hamamelidaceae, according to Hutchinson and Engler. The numbers are the basic chromosome numbers, so far as is known.

sets of six to make a 12 or the addition of an eight and a nine to make a 17; (2) the gradual stepping up or stepping down of the chromosome number by fusion and fraction of one or two pairs of the chromosomes in the previous set, that is, the derivation of an 11 chromosomed species from one with 12, etc. The whole subject is still in the experimental stage but it is at least far enough advanced to indicate that these two processes are among the main forces involved in the separation of genera in the higher plants. It will be seen that higher numbers may be derived

¹The Families of Flowering Plants. I. Dicotyledons. Macmillan and Co., London 1926.

²Gaiser, L. O. in *Genetic*, 12: 161-320 (1930).

³Sax, K. Published and unpublished work on chromosome numbers.

should be emphasized that the diagram is purely speculative. It has been worked out for those morphologists who would be interested in knowing how a cytologist with such information as is available would speculate as to the relationships of the groups involved. It might well be used as one of a set of possible working hypotheses by students of phylogeny. While the anastomoses of the main trunks of the Rosales stock represent supposed true-breeding allo-polyploid hybridizations, they do not necessarily indicate a cross between families as such. On any evolutionary hypothesis, related families derive, ultimately, from forms no more differentiated than present day genera or species. All that need be hypothesized for these hybrids is that they are between forms as diverse morphologically as certain hybrids which have been experimentally obtained, those between *Zea* and *Tripsacum*, for instance.¹ The diagram is based upon the evidence from chromosome number, secondary association and, in the case of the Pomoideae, from breeding experiments. It is much more speculative for the Saxifragaceae than for the Rosaceae. The Saxifragaceae, with base numbers of 8, 11, 13, 14, and 16 show a cytological complexity² paralleling their morphological diversity. Only a few of the fossil "dead branches" have been indicated. There must certainly have been many more. In this respect as in several others the actual details of the diagram are probably incorrect. The general conception, however, of a more or less webbed net-tree for the Rosales is strongly supported by the cytological evidence. In some other groups of the flowering plants (the Tubiflorae, for instance) the webbing would be so much more complex that one would scarcely use the word tree in describing it. In the Cyperaceae, on the other hand, there would be few if any anastomosing branches. The cyto-genetic evidence shows with increasing force that the actual pattern of evolutionary progress has been different in different groups of plants. The main point of the diagram in figure 3 is to suggest the general nature of the evolutionary pattern of the Rosales.

SUMMARY

1. Chromosome counts are given for nine species and six genera of the Hamamelidaceae.
2. The phylogenetic position of the family is discussed in the light of these results.

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¹Mangelsdorf & Reeves in Jour. Hered. 22: 329-343 (1931).

²Sax, K. in Jour. Arnold Arb. 12: 198-206 (1931).

CHROMOSOME STRUCTURE IN THE MEIOTIC CHROMOSOMES OF *RHOEO DISCOLOR* HANCE

KARL SAX

With plates 130 and 131

COILED CHROMONEMATA have been observed in both mitotic and meiotic chromosomes in various species of plants. The degree of coiling in mitotic chromosomes may vary from an irregular corrugation or loose spiral to a rather compact regular coil. At meiosis in certain plants the coils are much larger and can be analyzed in more detail.

The behavior of the meiotic chromosomes of *Rhoeo discolor* provides additional information regarding the nature of the coiled chromonemata. The observations are based on both aceto-carmin preparations and permanent smears fixed in Flemming's solution. In both cases the microsporocytes, after smearing, were usually pretreated with alcohol and ammonia before fixing. Immersion in tap water for a few seconds and a brief exposure to ammonia fumes also gave good results. This is essentially the method used by Kuwada. The ammonia vapor seems to dissolve the chromosome matrix and permit the spiral chromonemata to expand.

The chromosomes of *Rhoeo* are arranged in a ring or one or more chains at the first meiotic division. At early metaphase each chromosome contains a coiled chromonema consisting of two closely associated chromatids. The general appearance of these rings is shown in the photographs from aceto-carmin preparations (Figs. 1 and 2), but the finer details are best observed in permanent smears (Figs. 3 and 4). The number of coils is four or five per chromosome. At this stage the two chromatids are so closely associated that the coils appear to be single, but their double nature can be observed at certain loci. The diameter of the coil decreases gradually before the separation of the chromatids.

At late metaphase the coiled chromatids separate. The number of coils in each chromatid remains the same, but they are much smaller, even though there is little or no elongation of the chromosome as a whole (Figs. 5 and 6). At this stage both the terminal chiasmata and the fiber constrictions are very conspicuous, so that the order of the individual chromosomes in the ring can be determined. As observed earlier (Sax 1931), the order of the twelve chromosomes is always the same, thus supporting Belling's suggestion that such rings are the result of

segmental interchange. Six of the twelve chromosomes are distinctly heterobrachial, and the short arms are paired.

The meiotic chromosomes are always paired by terminal "chiasmata" and, in the chromatids at late metaphase, most of the chiasmata appear to be symmetrical. The chromatids are often parallel in several successive chromosomes or even in most of the chromosomes in the ring.

As the chromosomes pass to the poles at the first meiotic division, the chromatids separate except at the fiber constriction and become shorter (Fig. 7). During interphase the chromatids elongate considerably. At the second meiotic division they are about twice as long as they were at the first division. At this time the minor or somatic type of coiling can be observed. The coils are only about half as wide as the major coils found in the first division, and the number of coils is about 12 per chromatid (Fig. 8). These coils appear to be single at metaphase. There is some evidence of a split at late anaphase, as indicated by narrow regions at certain loci. If the chromatids are split at second metaphase, the two halves must be coiled together. At late anaphase they may tend to separate, but the slipping apart of the coils is difficult to detect except where there is a twist which appears to constrict the chromosome at such loci. More definite evidence of split chromatids has been obtained from microsporocytes which were subjected to low temperatures during development.

Under normal conditions the microspores receive six chromosomes, but occasionally there are seven, owing to irregularities in the first meiotic division. About 80 per cent of the microspores fail to develop, owing to segmental non-disjunction. The normal fertile microspores undergo a single nuclear division, followed by the differentiation of the daughter nuclei into the large and more or less degenerate tube nucleus and the compact elongated generative nucleus.

When the plants are kept at a temperature of about 6° C., two kinds of abnormalities appear. The chromosomes of the one nucleate microspore may divide but do not form daughter nuclei. The 12 chromosomes pass back into the resting stage and divide regularly at the next division to form diploid gametes. The other type of abnormal development begins when the low temperature inhibits chromosome pairing at meiosis. The twelve univalent chromosomes pass into the resting stage without nuclear division. They come out of the resting stage, divide without nuclear division and form a giant nucleus with 24 chromosomes, each of which consists of two coiled chromatids held together only at the fiber constriction (Fig. 9). Throughout this process the chromosomes never pass through the contraction characteristic of normal telophase stages.

The chromatid spirals are much looser than those found in the chromatids of the normal chromosomes at the second meiotic division, and it is perfectly clear that many of these chromatids are split. The splits are especially clear near the ends of the chromatids. At a somewhat later stage the two chromatids become completely separated, the chromatids elongate, and their structure is very clear. In the same chromatid one can observe the transition from a single coil to two parallel finer coils (Fig. 10). The mechanism of separation of daughter chromatids in these chromosomes, which are essentially of the somatic type, is similar to that found in the coiled chromatids in the first meiotic division.

The structure of the meiotic chromosomes in the permanent preparations was clear enough to permit an analysis of direction of coiling in the spiral chromonemata. We were able to determine the direction of coiling at all loci in each of the twelve chromosomes in 14 cells with complete chromosome rings. The classification of right- or left-handed spirals is purely arbitrary, since the direction depends on the sequence of determination in the ring. There is a strong tendency for the direction of coiling to be in the same direction in both arms of a chromosome. Of the 168 chromosomes examined, 50 had a right-handed spiral in both arms, 52 a left-handed spiral, and 66 showed a reversal of coiling, presumably at the fiber attachment. In only two chromosomes was there a second change of direction of coiling. Individual chromosomes could not be identified consistently, so that the direction of coiling could not be established for any one chromosome in all the different cells, but there is good evidence that direction of coiling is not a stable character. The number of chromosomes with left-handed coils ranged from 1 to 5, with reversed coils from 2 to 8, and with right-handed coils from 1 to 7, in different cells. The direction of coiling of chromonemata of paired adjacent chromosome arms is at random, with 85 coiling in the same direction and 83 coiling in reverse directions.

Both rings and chains of chromosomes are found at meiosis. If one or more chains are formed, the breaks may occur between either the long segments or the short segments. Three of the terminal chiasmata are formed between short segments, and eight of the terminal chiasmata are formed between long segments. The extra chiasma is between a long and a relatively short segment. The position of the breaks, or failure of chiasma formation, was obtained for 20 cells containing one or more chains. There were 9 breaks between the short segments and 16 between the long segments. These results suggest that chiasma formation is somewhat less likely to occur, or less likely to persist until late metaphase, between the short segments. The latter possibility is more probable

because we have found chromosome rings in practically all cells in some preparations.

The lengths of the chromosomes at different stages in meiosis were obtained to aid in the analysis of factors involved in chromosome contraction. It was not possible to get an accurate measurement of the length of the pachytene spireme in *Rhoeo*, but the total length is approximately 700 microns or an average of somewhat more than 100 microns per chromosome. The approximate average chromosome length at meiotic metaphase is 5–6 microns, and is about 9 microns at the second meiotic division.

THE MECHANISM OF CHROMOSOME CONTRACTION

The great contraction in chromosome length between pachytene and meiotic metaphase stages in *Rhoeo* is associated with the coiling of the chromonema. This coiling may not be the only factor involved. Belling (1928) believed that the approximation of chromosomes caused about one-third of the contraction in the chromosomes of *Lilium*, and that the coiling of chromonema effected the final shortening to give approximately a 10 to 1 reduction in length of the meiotic chromosome. Bridges (Alexander, 1928), on the other hand, assumed that coiling is the primary factor in chromosome contraction, and that the gene string maintains approximately the same length at all stages in the chromosome cycle. Another factor in chromosome contraction is the secondary or minor coils within the primary or major coils as described in *Tradescantia* by Fujii, Kuwada and Nakamura (1933) and found in *Sagittaria* by Shinke (1934).

We believe that three factors are involved in the great decrease in length of the meiotic chromosomes of *Rhoeo*; first, a linear contraction of the gene string; second, the major coiling of the chromonema; and third, the formation of minor spirals within the major spiral. The minor coils are not clearly differentiated at the first meiotic division in *Rhoeo*, but there is some evidence of loose coiling. The contraction of the chromonema and reduction in the width of the major coils between early and late metaphase are attributed to the further coiling of the minor spirals in each chromatid. A similar reduction in the major coils with no increase in chromosome length is found in *Secale* (Sax, 1930).

The coiled chromonema at early metaphase consists of two chromatids coiled together so that the chromonema often appears as a single coil, as is the case in *Tradescantia*, *Secale*, *Lilium*, and *Vicia*. The free separation of coiled chromatids has been explained by Kuwada (1927).

The reverse twists postulated by Kuwada can be observed in *Tradescantia* (Sax and Humphrey, 1934) and in *Trillium* (Huskins and Smith, 1935).

The direction of coiling in the chromonema spirals is more or less at random in *Rhoeo* and in *Tradescantia* (Nebel, 1932, Sax and Humphrey, 1934). According to Huskins and Smith, the paired meiotic chromosomes of *Trillium* usually coil in opposite directions, although no statistical evidence is presented, nor is there any adequate explanation for such behavior. Within a single meiotic chromosome the direction of coiling may change at the spindle fiber point, but is seldom reversed at other loci in *Rhoeo*, *Secale*, *Gasteria* (Taylor, 1931), *Tradescantia*, and *Sagittaria* (Shinke, 1934). Huskins and Smith find frequent changes in direction of coiling of anaphase chromosomes in *Trillium*. These changes in direction of coiling are usually associated with chiasmata. We have found changes in direction of coiling at chiasmata in the meiotic chromosomes of *Vicia*. If the chromonema coiling is caused by a contraction of the matrix, as suggested by Kuwada, the fiber attachment points and the chiasmata would tend to break any continuity of stress on the chromonema and changes in direction of coiling would be expected to be more or less at random at these points. There is a strong tendency, in both *Rhoeo* and *Tradescantia*, for the direction of coiling to be the same on both sides of the spindle fiber attachment, and only about one-third of the chromosomes show reversal of coiling at this locus. Huskins and Smith find that the reversals in direction of coiling between the fiber attachment and the distal ends of the chromatids at first anaphase is about twice the chiasma frequency at metaphase. This relation would be expected if the direction of coiling in homologous chromosomes is at random, and if reversals in coiling occur at random at the chiasmata.

In *Rhoeo* all chiasmata are terminal, and most of them appear to be symmetrical. The short chromosome arms are paired almost as frequently as the long arms. Changes in direction of coiling are rarely observed between the fiber and the distal end of the chromosome. These observations seem to indicate that chromosome pairing in *Rhoeo* is not dependent on the formation of interstitial chiasmata, but is dependent on a terminal association of homologous chromosome segments. This terminal association in certain rod bivalents in *Tradescantia* seems to involve the chromosome pellicle or matrix, but in *Rhoeo* there is evidence of fine chromatic connecting fibers.

During interphase the meiotic chromosomes of *Rhoeo* elongate but maintain some evidence of loose coils during the resting stage. At the

second meiotic division, a new spiral appears which has finer and more numerous spirals than the major coils at the first meiotic division. These minor spirals have been described in *Lilium*, *Rhoeo*, *Allium*, *Tricyrtis*, *Najas*, and *Hosta* by Shinke (1930), and in *Tradescantia* by Nebel (1932), Kuwada and Nakamura (1933) and Sax and Humphrey (1934). These coils in *Rhoeo* are wider than the minor spiral within the major spiral at the first meiotic division and presumably are formed independently during the prophase of the second meiotic division. These spirals are much like those found in certain somatic chromosomes. The transition from about five major spirals to 20–25 minor spirals in the successive meiotic divisions in *Tradescantia* and a similar behavior in *Rhoeo* is difficult to reconcile with the "heterogonic growth" hypothesis of spiralization suggested by Huskins and Smith.

The anaphase chromosomes at the second meiotic division have been described as two-parted in a number of plants (*Gasteria*, Taylor, 1931; *Galtonia*, Smith, 1932; *Tradescantia*, Nebel, 1932; *Trillium*, Huskins and Smith, 1935; et al.; Cf. Sharp, 1934). Both Kuwada and Nakamura, and Sax and Humphrey found only single coils in the second anaphase chromosomes of *Tradescantia*. In *Rhoeo* there is evidence that the anaphase coil is double, but that the two half-chromatids are coiled together so intimately that they appear as a single coil at early anaphase. As the coils begin to separate the gyres are matched so closely that the dual structure is not clear, but where a twist occurs there is a narrow region in the chromosome. The abnormal "microspores" of *Rhoeo* show the chromatid splits clearly in various stages of separation. The minor coils, characteristic of somatic chromosomes, are similar in structure to the major coils; the two chromatids (or half-chromatids) are coiled together in parallel in such a manner that they can separate freely without entangling. If the split occurs while the chromosome is coiled, there must be some lateral polarity so that the division occurs in only one plane parallel to the axis of the chromosome, as Nebel (1933) has suggested.

If there is a chromatid split in the anaphase chromosomes of the second meiotic division in *Tradescantia*, the chromatid must behave as a single unit until midprophase of the microspore division. *Tradescantia* microspores subjected to x-rays show chromatid breaks for about two days after raying, but after three or four days only chromosome breaks are observed at metaphase (Riley—unpublished).

We find that either abnormally low or high temperatures will cause nuclear irregularities. These include failure of chromosome pairing at

meiosis, chromosome division without nuclear division, and failure of normal differentiation of nuclei. Since these temperatures are within the range occasionally experienced in nature, it is probable that temperature fluctuations have played an important part in chromosome changes in nature (Cf. Randolph, 1932). This work with temperature effects has been aided by a grant from the American Academy of Arts and Sciences.

SUMMARY

The twelve chromosomes of *Rhoeo discolor* are arranged in a segmental interchange ring at the first meiotic division. Each chromosome contains a spiral chromonema consisting of two chromatids coiled together. There is some evidence, both direct and indirect, that there is a minor spiral within the chromatids of the major spiral. During metaphase the major spirals become smaller, and the two chromatids separate. The chromosomes elongate greatly during interphase, but there is evidence of a spiral structure during the resting stage. At the second meiotic division, new minor spirals are formed which are smaller and more numerous than the major spirals of the first division. The chromatids at anaphase of the second meiotic division are split, but the two half-chromatids are so closely coiled together that they are not easily observed. They can be differentiated easily in cells where the normal chromosome cycle is disturbed by subjection to low temperatures.

The reduction in the length of the meiotic chromosomes of *Rhoeo*, between prophase and first metaphase is attributed to three factors:— a linear contraction of the gene string, the coiling of the chromonema into major coils, and the development of minor coils in the chromatids of the major spirals. The direction of coiling in the major spirals seems to be at random. In a single chromosome the direction of coiling may change at the fiber attachment point, but it is seldom reversed at other loci.

The meiotic chromosomes are paired at the ends, apparently without the formation of interstitial chiasmata.

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EXPLANATION OF PLATES

PLATE 130

- Meiotic chromosomes of *Rhoeo discolor*. Figs. 3 and 4 from permanent smears. All others from aceto-carmin preparations. $\times 2000$.
- Figs. 1 and 2. The coiled chromonemata in the chromosome ring at early metaphase.
- Figs. 3 and 4. Coiled chromonemata showing reversal of coiling and reduction in width of coiling at metaphase.
- Figs. 5 and 6. Separation of coiled chromatids at late metaphase. The same number of coils are found in the coiled chromatids as in the coiled chromonemata, but the spirals are smaller.
- Fig. 7. Telophase of first meiotic division.
- Fig. 8. Chromosomes at the second meiotic division showing minor spirals which appear to be single.

PLATE 131

Chromosomes from abnormal "microspores" produced by chromosome multiplication induced by cold treatment. Magnification $\times 2000$.

Fig. 9. A giant cell derived from a microsporocyte by chromosome division without nuclear division. Each of the 24 chromosomes consists of two chromatids held together at the fiber attachment. Many of the chromatids are split.

Fig. 10. Chromatids at a somewhat later stage showing the transition from a single coiled chromatid to two coiled daughter chromatids.

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CHROMOSOME STRUCTURE IN MEIOTIC CHROMOSOMES
OF *RHOEO DISCOLOR*



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CHROMOSOME STRUCTURE IN MEIOTIC CHROMOSOMES
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ELAIOPLASTS IN IRIS: A MORPHOLOGICAL STUDY

ANNA F. FAULL

With plates 132 to 137

INTRODUCTION

ELAIOPLASTS are a heterogeneous group of intracellular bodies presenting the characteristics of fatty substances to a marked degree but not recognizable as ordinary types of plastids, chondriosomes or vacuoles. There is no general agreement in the literature regarding their structure, origin, development, classification or chemical composition. They have been variously described as aggregations of lipoid globules, as modified or unusual types of plastids or vacuoles, as nuclear derivatives, as aggregations of mitochondria-like bodies or as independent structures. They have been linked with various physiological processes such as assimilation, excretion or degeneration.

Much of the confusion regarding elaioplasts is due to the use of inadequate techniques and to a consequent lack of accurate information about the early developmental stages of these bodies. Many of the discrepancies are also due to failure to visualize and interpret correctly the full range of morphological variability of chondriosomes and plastids.

The investigations described in this paper were undertaken to clarify our conception of the elaioplasts in *Iris* and to compare these bodies with those in other monocotyledons and in liverworts. By using an improved technique critical evidence has been obtained to show the early stages in the development of the elaioplasts in *Iris* and the changes which these bodies undergo in different tissues and at different seasons.

In addition to the morphological study an extraction and preliminary analysis of the so-called oil in the elaioplasts of *Iris* and some physiological experiments on the metabolism of two types of *Iris* rhizome, one of which contains abundant elaioplasts, have been made. The results of these investigations are being published elsewhere.

HISTORICAL RÉSUMÉ

Since the middle of the last century papers have appeared from time to time describing cytoplasmic bodies associated with oil. The writers have used various names for these structures which through usage have become more or less interchangeable. Thus they are termed elaioplasts,

oléoplasts, oléosomes, ölkörper, oil bodies, Zellenbläschen, Zellenkörper, fatty bodies, elaiosferer, oelplastids, oléoleucites, éléments oléifères and système oléifère. Sometimes the terms are restricted in their application. For example ölkörper is used only for oily bodies in the liverworts, and elaioplast is kept for those in the monocotyledons. But recently with an increasing tendency to consider all of these oily bodies essentially similar, one name is often used to designate all of them.

The earliest references to elaioplasts are found in the writings of Mirbel (35) in 1835, of Gottsche (13) in 1843, of Holle (24) in 1857, of Hofmeister (23) in 1867 and of Ward (49) in 1883. But the first adequate descriptions of oil bodies were published in papers by Pfeffer (38) in 1874 and by Wakker (47) in 1888. These, together with a paper by Lidforss (32) in 1893, provide a description of the three main types of mature oil bodies; from this later authors have diverged little. Although often resembling one another, the three main types present certain distinct features which are further emphasized by their restriction to a given group of plants.

Pfeffer (38) described oil bodies characteristic of the liverworts. In common with such bodies in general, they are highly refractive structures which stain brilliantly in "fat" dyes, such as alkannin, and which are more or less soluble in 95% alcohol and in fat solvents such as ether. They are distinguished from other oil bodies by their almost complete solubility in alcohol, by a characteristic residual ring left after treatment with alcohol, by their location commonly in the peripheral cytoplasm but within the chloroplast-bearing layer, by their presence in practically every species of the group, by their appearance commonly in every cell of a plant and by their permanency as cell structures. The Marchantiales present a contrast to other elaioplast-bearing hepatics in the restriction of the oil bodies to special cells scattered throughout the thallus and in the location of a single large oil body in the center of each of these cells. Oil bodies in the liverworts vary in shape from round to spindle-shaped as a rule, though some are irregular in form. They vary in color from colorless to dark brown and in appearance from granular to segmented or homogeneous.

The oil bodies described by Wakker (47) differ from those in the liverworts in their location near the nucleus, in their invariably granular appearance, in their often irregularly lobed shape, and in their character of being more or less temporary cell structures. Elaioplasts of this type are often yellowish in color and are marked by their reaction with some reagents which cause an extrusion of the oil and leave a characteristic net-like structure. Although reported from most tissues, they

are often restricted to certain ones. Raciborski (41) and Beer (4) found them only in flower or fruit tissues, while Politis (39) described them in these tissues and in those of bulbs. Oil bodies of this type are further restricted to a few groups of flowering plants. Lists published by Zimmermann (51) and by Politis (39) record them in groups of species in the Orchidaceae, Liliaceae, Amaryllidaceae, Iridaceae and Malvaceae, while Beer (4) found them in one of the Compositae.

The third type of oil body described by Lidforss (32) is characterized by its homogeneous appearance, by its spherical shape and by its unrestricted location in the cell. It is reported from leaf tissues of flowering plants and is of common occurrence in this group.

Besides these three classes of oil bodies there are isolated descriptions of elaioplasts that are not included in any of the types described. Such are the reticulate, highly refractive structures saturated with an amber-colored oil described by Keene (26, 27) in two molds. Such also are the yellow, green or black oil bodies near the nucleus found by Hieronymus (22) in some algae.

In 1888 Wakker (47) demonstrated by abnormal plasmolysis that the oil bodies in the monocotyledons and in the liverworts are located in the cytoplasm. He showed that, although these structures often protrude into the vacuole, they are never located in it as Pfeffer (38) and Rattray (42) had thought. Later investigations have substantiated Wakker's observations and extended them to include all types of elaioplasts.

There is no general consensus of opinion on the structure of the non-homogeneous oil bodies. Pfeffer (38) described them as aggregations of homogeneous oil globules, a view expressed in modern times by Guilliermond (20), by Meyer (34) and by Kozlowsky (28). Other students have described a stroma with embedded oil globules. This view was first expressed by Wakker (47). It was elaborated upon by Zimmermann (51), who pointed out less refractive inclusions which he termed vacuoles or portions not producing oil. Later Beer (4) and Politis (39) described the elaioplasts in *Gaillardia* and in the monocotyledons as aggregations of smaller bodies, each composed of a stroma with included oil globules. A more elaborate structure was postulated by Woycicki (50) and by Keene (26, 27). Woycicki described elaioplasts in *Vanilla* with central oily drops surrounded by a mucilaginous layer which in turn was covered by a granular layer. Keene described a somewhat similar structure in the oil bodies of *Sporodinia* which showed a denser reticulate center and a coarser reticulate outer portion. The presence of an unfixable stroma in the oil bodies of the liverworts in

contrast to the fixable one in those of the monocotyledons was pointed out by Küster (29). Later Gargeanne (9) and Dombray (7) attempted to show that this unfixable stroma was a fluid or a semi-fluid.

The question of an enveloping membrane has been raised with reference to the oil bodies in the liverworts. Pfeffer (38) inferred the presence of a membrane from the characteristic ring left after treatment with alcohol. Küster (29) demonstrated in 1894 that this ring is an artefact. Gargeanne (9) repeated the demonstration but maintained that, although the ring is an artefact, the bodies possess a true membrane homologous with the tonoplast of the vacuole. Later writers have not agreed with Gargeanne in recognizing a membrane. The presence of a membrane about elaioplasts in the monocotyledons has been described only by Raciborski (41) who considered the stroma at times to be reduced to a surrounding layer.

The development of the oil bodies is also a disputed point in the literature. Pfeffer (38), Rivett (43), Lidforss (32), Chalaud (5), Meyer (34) and Guilliermond et al. (20) have considered the formation of elaioplasts to be a process of aggregation of small drops in the cytoplasm with more or less fusion. Kozlowsky (28) has further stated that the drops are first extruded from the chloroplasts. A second theory has been postulated by Wakker (47), by Küster (29) and by Harper (21). They consider that a stroma appears first as a shadowy, wrinkled structure in which refractive oil drops appear later. Gargeanne (9) stated that the oil drops are secreted by a surrounding membrane, while Dombray (7) described the deposition of substances from the cytoplasm and their transformation by the cell sap as a catalyser. Another theory is expressed by Hieronymus (22) and by Beer (4) who described elaioplasts formed by the aggregation of degenerating plastids with the production of oil. Somewhat similar is Woycicki's (50) theory of the aggregation, partial degeneration and fusion of mitochondria-like bodies forming oil. Keene (26, 27) postulates the formation of a reticulate structure in homogeneous bodies with the later fusion of several of these bodies. Still another theory by Politis (39) and by Raciborski (41) describes the development of elaioplasts by the growth of refractive drops and the subsequent fusion of the bodies so formed.

The division of elaioplasts has been noted in a few instances. Raciborski (41) in 1893 described a fragmenting of the bodies after they had passed maturity and a breaking off of bud-like protrusions. Again in 1914 Politis (39) described division of the elaioplasts. Politis considered division not merely an incidental or degeneration phenomenon, but a method of increasing the number of these bodies. Besides the

budding already described by Raciborski, Politis described passive division of the body by the cell wall during cell division.

The history of oil bodies after they have reached maturity has been studied. In the liverworts they are generally thought to remain unchanged even after the death of the cell, although Dombray (7) noted a decrease in size, fusion of the oily globules and aggregation of the oil bodies before death. Elaioplasts in the monocotyledons are generally thought to degenerate some time after reaching maturity. Wakker (47) described their disappearance in older tissues of *Vanilla*. Beer (4) and Woycicki (50) described a resolution of the oil bodies into scattered oily spheres. Politis (39), on the other hand, described the disappearance of the oil first, leaving a vacuolated protein mass which might later disappear also.

Movement has been noted in connection with elaioplasts. In 1893 Zimmermann (51) first recorded the rotation at times of oil bodies in the monocotyledons, a phenomenon observed also by later investigators. A second type of motion consisting of Brownian movement of the globules within the oil bodies appears in oily structures in the hepatics. Gargeanne (9) described this as an injury phenomenon, but recently it has been noted by Dombray (7) as a normal condition in the elaioplasts of some species.

The chemical composition of the elaioplasts and particularly of the oily portion has received much attention. The theories advanced are based chiefly upon microchemical reactions. Dombray (7) has interpreted microscopical observations in the light of analyses of extraction products. Two opposing theories regarding the composition of the oil have been formulated. In one the oil is said to be chiefly a mixture of essential oils. This is the view recently expressed by Popovici (40) and by Rivett (4) in her description of the oil as a mixture of essential oils with small amounts of protein and fatty oils. Dombray (7) stated that the oily substance was a mixture of essential oil and "tannoides." The opposing theory considers the oil to be composed chiefly of fatty oils. This is the opinion of most investigators. Pfeffer (38) described the oil as a mixture of fatty oil with some water and protein and with traces of wax and resins. Later Küster (29) designated the oil in the elaioplasts of liverworts as a fatty oil resembling castor oil. Lidforss (32) identified the oil in the homogeneous oil bodies of flowering plants as a non-drying oil containing fatty acids of the type $C^n H_{2n-2} O_2$. The stroma, if present, is generally considered to be a protein, a view first expressed by Zimmermann (51).

There is little agreement among investigators concerning the origin

and identity of oil bodies. Raciborski (41), Küster (29) and Gavaudan (10, 11, 12) have considered them to be cell systems independent of the vacuome, chondriome or plastidome and originating more or less *de novo* in the cytoplasm. Wakker (47) considered them to be special plastids, while Beer (43) and Hieronymus (22) described them as degenerating plastids. Kozłowsky (28) has stated that they are products of the chloroplasts. That they are special or transformed vacuoles has been postulated by Keene (26, 27), by Dombray (7), by Gargeanne (9) and by Rivett (43). Woycicki (50) and Lundström (33) have described oil bodies originating from mitochondria-like bodies. Politis (39) has ascribed a nuclear origin to them.

A relationship between elaioplasts in the monocotyledons and crystal formation has been suggested. Wakker (47), Politis (39) and Monteverde (36) stated that there is no connection between the oil bodies and the calcium oxalate crystals found in the same plants. But Warlich (48) considered them to be interdependent structures, while Woycicki (50) in 1929 described crystals forming in some of the elaioplasts in *Ornithogalum*.

Many writers have ventured theories on the physiological and biological significance of the oil bodies. In general they have considered those in the liverworts and also the homogeneous ones in the flowering plants to be excretions. But those in the monocotyledons they term assimilation products, although Raciborski (41) stated them to be excretions. Various other theories have been offered. Beer (4) in 1909 demonstrated that the bodies in *Gaillardia* are degeneration products of the plastids with the secondary function of producing color. Hieronymus (22) and Lundström (33) suggested that the bodies are protective in function, a theory opposed by Dombray (7).

In concluding the summary of the literature on oil bodies it should be noted that these structures do not include the ölplasma described by Leiner (31) and by others of Tschirch's school, nor do they include the oil cells described by Lehmann (30) and others. The former (ölplasma) deals with oil in the cytoplasm — chiefly of fatty seeds. The subject is well summarized in the account by Tunman and Rosenthaler (46). The phenomenon of the appearance of oil in special oil cells involves the transformation of large portions of the cytoplasm or secretion from the modified cell wall rather than the appearance of oily bodies in the cytoplasm.

In addition to the literature on oil bodies, some reference should be made to the literature on the structure of Iris cells. The most recent and complete studies are those by Guilliermond (15-20) and by Dan-

geard (6). They have developed a method of vital observation especially adapted to this type of study. They have pointed out the presence in *Iris* cells of vacuoles and their inclusions, of cytoplasm, of oil globules, of chondriosomes of various types and of plastids. In particular Guilliermond has described the chondriosomes and plastids and their developmental stages. He has noted the presence of oil globules in most plastids and chondrioconts in *Iris*. These globules which he has found associated more often with young or degenerating types of plastids he considers to be lipoids separating out from the plastid substance. He has described the development of plastids from mitochondrial types differentiated from other mitochondria by their potentiality for plastid formation. He has described the formation of chloroplasts from an intermediate chondriocont stage by budding and fragmenting. Other phases of studies carried out on *Iris* include the action of hypo- and hypertonic solutions on chondriosomes, observations of the amoeboid movements of chondrioconts, and the identification of an oily body in the vacuoles of certain cells as a phenol compound.

MATERIAL

The plants used in my studies of elaioplasts included numerous irises, some liverworts and a few representative flowering plants. They were obtained from several sources. The major part of the study was made on colonies of *Iris versicolor* and of an *Iris pallida* of hybrid origin which grew in abundance near the laboratory. For work on living tissues it was desirable to have the plants as close at hand as possible. It was also desirable to locate single colonies in a natural habitat for the basic study of variations. In this way differences due to season, development, etc., were less likely to be confused with those due to location, to abnormal habitat or to individual variations.

As a rule the material was used as soon as it was collected. But in some instances it was kept in water or in wet sand in the greenhouse for later observations, or it was transplanted to garden beds. In the early part of the study a few plants of *I. pallida* and of *I. versicolor* were transplanted to pots in the greenhouse to supplement the outdoor material. Although some interesting observations were made on these plants, they grew so poorly that this method of providing material was abandoned. Fortunately, it was not necessary to rely on greenhouse or garden material at any period.

The *Iris versicolor* was taken from a swampy field at the corner of Weston St. on the Cambridge-Concord turnpike about an hour's drive from the laboratory. The *Iris pallida* hybrid, a garden plant, grew in

beds within a few rods of the laboratory. Both of these species were sufficiently near at hand to be obtained as they were needed for examination.

The other irises used as supplementary material and for a general survey of the genus were obtained from several places. A group of native West Coast species was studied in California. Three of these, *I. macrosiphon*, *I. Douglasiana* and *I. longipetala*, grew naturally within a few hours' drive of the laboratory. But *I. Hartwegii* and *I. missouriensis* had to be brought to Palo Alto from the eastern part of the state. A large number of other species were obtained from the Missouri Botanical Garden, from the Brooklyn Botanical Garden and from the New York Botanical Garden. Those at the Missouri Garden were examined *in situ*, but the ones from New York were brought to Boston for examination.

For a list of the species of *Iris* studied see the table on page 246.

In addition to the *Iris* plants, a group of rhizomatous plants and a number of liverworts were obtained. The former were studied at the Missouri Botanical Garden for the most part, although a few were collected around Boston. Two species of *Vanilla*, the plant used by Wakker (47) in his classical studies on elaioplasts, were obtained from Panama. The liverworts were collected in the New England woods for study in Boston or they were sent from Oregon to the California laboratory for use there. The hepatics were kept in the laboratory in moist glass containers over a period of weeks.

A list of the flowering plants studied is given on page 248 and one of the hepatics on page 254.

TECHNIQUE

In choosing a method for the morphological examination of the elaioplasts one fundamental requirement was kept in mind. It was desirable to observe the bodies in as unaltered a condition as possible in order to discover their normal development and variations due to seasonal, environmental or specific differences in the plants examined.

At the present time there are two methods used in the study of cytoplasmic bodies. The first of these is the fixation technique introduced in the later decades of the nineteenth century and developed to the highest degree in the complicated "mitochondrial techniques" and "silver or osmic impregnation methods." Essentially it consists of killing and fixing blocks of tissue in reagents that solidify proteins and fats, rendering them insoluble in specific fluids, and then staining sections differentially. Incidentally the technique involves a rather complicated process of embedding and one or more dehydrations.

The other method is that of examining untreated tissue either with or without the aid of vital dyes. Although untreated tissue was used before the introduction of fixatives, it was superseded by them. Recently the so-called vital technique has been revived and developed, notably by the Dangeards and by Guilliermond in France and by Bailey in America. Guilliermond has described a technique for vital staining in his studies of the vacuome and has contributed data on various aspects of injury and death in his studies of the chondriome. Bailey (1) in his investigations of the cambium has tabulated criteria that can be used in distinguishing living from dying or dead cells. Bailey and Zirkle (2, 3) have clarified the vital staining technique by their investigation of the toxicity of a large number of dyes, of the most suitable media in which to use the stains, of the staining properties of different dyes and of the varying reaction of vacuoles to given stains.

Both of these methods were tried in the study of *Iris*, but that of fixation was eventually discarded because of the difficulties involved. The vacuoles in the rhizome were found to contain large quantities of a substance that precipitated with fixatives and stained deeply, obscuring the sections, while the elaioplasts in the rhizomes of *Iris versicolor* contained quantities of "oil" that either was dissolved or was extruded in large masses obscuring the cell structure. In the one or two instances where this did not occur, a good fixation was obtained in mature but not in meristematic cells. The fixation images in sections of rhizome meristem were not comparable with those obtained in root-tip meristems, nor could they, as in the case of the root-tips, be identified with structures clearly seen in similar "living" cells. A third difficulty, that might in time have been overcome, lay in the persistent plasmolysis of cells in the rhizome meristem and in leaf tissue. For these reasons it was felt that the fixed material did not give an image of unaltered cells, nor could it be relied upon for comparative work. Better results were obtained with the "vital" technique where dead and dying cells could be observed and where those that survived for some hours without undergoing lethal changes seemed to present a more reliable picture of an unaltered condition. Consequently after some months of unsuccessful experimenting with fixatives and dehydrating reagents and with different hydrogen ion concentrations of single fixatives, the method was entirely abandoned and the "vital" technique alone retained.

Although fixation methods were finally discarded, it should be noted that in certain instances satisfactory results were obtained in this way. Thus the mitochondrial fixatives and stains proved successful for root-tips where they apparently produced little or no alteration in the cell

structure. Likewise, since chromic and osmic acids fixed the elaioplast "oil," occasional slides were obtained of mature rhizome tissue quite comparable with that examined "vitaly." Other fixations, although they did not give exact images of the cytoplasmic contents of the cell, proved useful in determining the structure of the oil bodies. The fixatives that proved most successful for the occasional rhizome slides were 0.5% osmic acid solution and Flemming's weak solution followed by Flemming's triple stain. The most satisfactory of the mitochondrial fixatives was ammonium Erliki solution (25 cc. each of 1% solutions of ammonium and potassium bichromates plus 25 cc. of an 8% solution of formaldehyde) followed by Milovidov's modification¹ of Volkonsky's stain. With these fixatives the usual dehydrating and paraffin embedding schedules were satisfactory. A third instance of useful fixation was found for the mitochondrial fixatives. These, although not entirely successful except for root-tips, did fix mitochondria throughout the plant sufficiently well for a rough survey of the distribution of these elements.

The "vital" method was preferred and finally used exclusively because it presented a more reliable picture of unaltered cell structures. Although this was the main consideration, there were other factors that made the "vital" technique especially favorable for the study of developmental and other changes within the cell. Of primary importance was the possibility of observing fluctuating changes of a moment's duration, as well as those more permanent ones associated with age or season. This was possible only with a technique which left the more or less fluid contents of the cell unchanged. The "vital" method provided such a technique. Another factor favoring the "vital" method was its practical simplicity. Although some skill was required in sectioning, after this was obtained the actual preparation required but a few seconds. Not only was this a saving of time but it was possible to examine material as it was brought in, a method that enabled one to proceed quickly with the study. A third factor of importance was the applicability of the method without modification to all kinds of material. In a comparative study of tissues and plants this was an essential requirement for the technique.

As used in this study the "vital" technique was essentially that developed by Bailey (1) for the study of cambium. The material was

¹Stain in acid fuchsin over flame for 5 min.; stain in 0.5% aurantia in alcoholic solution for 20 min.; stain in gentian violet; differentiate in alcohol. [Milovidov, P.F. Sur les méthodes de double coloration du chondriome et des grains d'amidon. — *Archiv. Anat. Micro.* (24), 1:9. 1928.]

sectioned, placed in appropriate solutions and examined immediately and at intervals. For distinguishing the living from injured or dead cells criteria were established based upon comparisons between obviously injured cells and those that survived for some hours before showing signs of injury. The only differences in the technique for *Iris* lay in the details of sectioning and of preparing solutions and in the possibility of more firmly establishing criteria for living cells by comparisons with mounts of thin, unsectioned tissue.

The sectioning was done with a "Gem" razor blade freehand, or, for some rhizomes, with a Thomson-Spence sliding microtome. Although the microtome sections were more uniform in thickness and more convenient for mature rhizomes, they were less satisfactory with the other tissues. Apparently a thinner blade produced less injury in rhizome meristems, while it was the simplest means for sectioning leaf, flower or root tissue. The razor blade was used for mature rhizomes also when a microtome was not available. In either case, sections were obtained varying from one to several cells in thickness. Measured by the microtome, sections of mature rhizome varied from 30 μ to 50 μ or more, while those of the smaller-celled meristem were 15 μ to 20 μ or less.

The solutions in which these sections were immersed consisted of a basic solution plus one or more of the "vital" dyes, or merely of the basic solution alone. Of the three fluids tried, water, nujol and sucrose solution, the sucrose solution in a five to ten per cent concentration, proved most satisfactory.

The dyes most commonly used were Neutral Red, Janus Green BB, Chrysoidin Y and Benzene-azo-alpha-naphthylamine. Although Chrysoidin Y is the only one of these dyes which stains the elaioplasts, the light staining of the vacuole with Neutral Red throws the cytoplasm into relief and makes its structures more clearly visible. The other dyes in combination with Neutral Red and Chrysoidin Y have a clarifying effect. None of these dyes stain the immature oil bodies, while the staining of the mature oil bodies by Chrysoidin Y is but temporary. Almost all dyes will stain dead, mature oil bodies. In practice, only traces of the dyes were used (one drop of a concentrated aqueous solution to 25 cc. of sugar solution). Staining is better and more rapid when the sucrose solution is made alkaline with Clark's buffers (pH 8.2 to 8.6) which shorten the staining period from an hour or more to fifteen minutes or less. Since most stains, even in small amounts, are toxic after a time, sections that it was desired to keep were removed to pure sucrose solutions. In this way cells were kept "living" for twelve hours or more.

An essential part of the technique was the establishment of criteria

for distinguishing living from dead or dying cells. By comparing obviously injured cells with those which survive sectioning for some hours without sign of injury, such criteria have been established for cambial tissue. By the same method criteria were found for *Iris* cells. In addition unsectioned roots, bracts and flower parts of *Iris* and the thin leaves of a *Potamogeton* were examined. Living cells in *Iris*, like those in cambium, are marked by the following characters: regular cyclosis, absence of Brownian movement in the cytoplasm and a staining of the vacuole in the presence of Neutral Red. Two additional criteria were found for living cells of *Iris*, namely, a pulsation of the cytoplasm in isodiametric cells and the amoeboid movement of the chondriosomes. Both of these phenomena are essentially a swelling or contraction of parts of the structure involved. The pulsation, for example, is the swelling of one part of a protoplasmic thread at the expense of another, a phenomenon involved in changes in the concentration of the substance at a given point. The pulsation of the cytoplasm occurs principally in isodiametric cells where there is no streaming. The amoeboid movement of the chondriosomes may occur in any cell. Both criteria proved valuable as indications of the condition of the cells. Dead cells of *Iris*, as of the cambium, show one or more of the following characteristics: coagulation of the protoplasm, a general formation of granules in the cytoplasm, staining of the nucleus and cytoplasm in the presence of dyes, increasing opacity of the whole cell and Brownian movement in the cytoplasm. Dying cells in *Iris* were found to show the following characters: jerky or irregular streaming and Brownian movement within the plastids. Parallel phenomena were found in the irregular streaming and degenerating plastids of some epidermal, bract and flower tissues.

The validity of these criteria for distinguishing living from dying or dead cells should be considered. The possibility of injury lies in the sectioning, in the action of the solutions in which the sections are placed, in the pressure of the cover glass used in mounting sections and in the strong light used for microscopic observations. In establishing criteria, the use of unsectioned material eliminated the possibility of injury due to sectioning, while the examination of water plants in the water of their natural habitat provided a check upon the effects of the solutions used in the study of *Iris*. A similar check upon the effects of pressure from the cover glass was provided by removing it. The possibility of injury due to strong light alone remains. That strong light will produce injury and death is clear, but the effects are slow in appearing and, if the light is removed in time, they are temporary. They can be taken

into account in establishing criteria for distinguishing living from dying or dead cells. That there are undetected, instantaneous changes is improbable, for the reactions in plants are in general slow. The effect of the light appears chiefly in the slowing down of streaming, and, if exposure is continued, unmistakable signs of death such as coagulation of the cytoplasm finally are observed.

It should be noted that the observation of minute details of cytoplasmic structures can be carried on only with the aid of the best high-powered microscopic equipment. For the observation of sections mounted in aqueous media a water immersion objective is essential. Without such equipment, many of the details of structure described in the following section cannot be seen.

OBSERVATIONS

DESCRIPTION OF ELAIOPLASTS IN RHIZOMES OF *IRIS VERSICOLOR*

Elaioplasts occur typically in the parenchyma of the rhizomes of *Iris versicolor*. They appear in every cell as granular, highly refractive masses with a decidedly yellowish cast (Fig. 1). The individual elaioplasts are almost spherical in shape and seem to be composed of closely compacted globules approximately one micron in diameter (Fig. 2). They are relatively constant in size within a given rhizome, generally averaging 10 to 13 microns in diameter. Although in some material they may be twice this size, they are never as large as the nucleus which has a diameter of the order of 40 to 50 microns. Often a hundred or more of these elaioplasts will be found in a single cell, aggregated for the most part into one large mass. Sometimes there are as few as twenty to a cell, but often they more than half fill the cell lumen, obscuring the nucleus and protruding into the huge vacuole.

All evidence shows that the elaioplasts are located in the cytoplasm. Although they protrude into the vacuole, protoplasmic threads are often observed to spread at their surface as if to include them (Fig. 1). Occasionally one is seen moving in the streaming protoplasm. The study of similar bodies in the root, where they obviously are included in the cytoplasm, substantiates these observations.

Microchemical tests indicate that the bodies are mainly lipid in character. They stain brilliantly in "fat" dyes such as Sudan III, alkannin and nascent indophenol blue.¹ They are almost completely

¹For this technique see Zweibaum, J. Sur la coloration des graisses dans la cellule vivante. Comp. Rend. Soc. Biol. 1923. — Zweibaum, J. and G. Mangenot. Application à l'étude histochimique des végétaux d'une méthode permettant la coloration vitale et post vitale des graisses de la cellule végétale. Comp. Rend. Soc. Biol. 1923.

soluble in lipid solvents such as ether, chloroform and carbon tetrachloride. They also dissolve largely in 95% alcohol, a solvent for some oils. They are insoluble in hydrochloric acid, sulphuric acid and potassium hydroxide, although they are more or less structurally disorganized by these reagents. They are not volatile at 100°C., which indicates the presence of lipoids rather than essential oils..

The reaction of the elaioplasts to heat and to many reagents in which they are insoluble is marked by the extrusion of the lipid in drops (Fig. 5). The reaction occurs relatively slowly so that it can be watched. A net-like residue remains which is not distinctly lipid in character. The drops characteristically remain in contact with the net and are flattened on their attached side. The reaction occurs with heat, picric acid, dilute sulphuric acid, Gram's solution, etc.

Injury to the cell typically produces active Brownian movement of the globules within the limits of the elaioplast which eventually bursts, freeing the globules within the cell lumen. A similar phenomenon occurs in elaioplasts which escape from cut cells. It can be induced by mechanical pressure.

STRUCTURE OF ELAIOPLASTS IN RHIZOMES OF *IRIS VERSICOLOR*

The structure of the elaioplasts in the mature rhizome is that of a matrix with embedded globules. This is best shown in sections of fixed material, for the globules in fresh material are so refractive and so closely packed that it is difficult to distinguish any structure clearly. With osmic acid and some of the chrom-osmic fixatives the globules are preserved *in situ* (Fig. 3b). They clearly show a network of a different substance between them. With other fixatives the globules are never preserved, but a net-like structure with lacunae of the approximate size of the globules remains (Fig. 3a). This can be seen best by the use of mitochondrial or plastid fixatives such as ammonium Erliki and an appropriate stain. It is well shown, too, by Wakker's method for double staining elaioplasts with anilin blue and alkannin after fixation of sections in picric acid. In this case, the extruded globules are stained red and the matrix appears as a purple network with blue interstices.

The behavior of the bodies in fresh material supports the observations on their structure as seen after fixation. The globules show no tendency to fuse, a fact which indicates a separation by the presence of at least a surface film. In injured material, they move apparently unchanged in a liquid portion of the intact body. Further proof of a matrix is found in developmental forms and in homologous oil-bearing

bodies in other species. Here the matrix is often so abundant as to be clearly visible in untreated material. Such is the case in very young cells of the rhizome, in some cells of the root-tip, in rhizomes of *Iris pallida* and of *Iris Hartwegii*, etc. The matrix is also clearly shown in the root during the degeneration of elaioplasts. Here before death the refractive globules disappear only a net with lacunae. This net is very similar in structural appearance, although not in shape, to the net-like image of rhizome elaioplasts in fixed material.

The globules were identified as the material which gives the elaioplast as a whole its lipid characters. They show the reactions previously described for the elaioplasts and additional ones equally characteristic of lipoids. They stain in the "fat" dyes. This is apparent in intact bodies, but it is more clearly seen with the moving globules in disintegrating ones. They are highly refractive, a property seen in both intact and disintegrated elaioplasts. They disappear from sections treated with "fat" solvents such as carbon tetrachloride, ether, etc., but they may be preserved in sections treated with "fat" fixatives such as osmic acid and chrom-osmic mixtures. They are completely soluble in alcohol. This was demonstrated with globules in suspension in alkaline water. Upon the addition of 95% alcohol a homogeneous fluid resulted indicating the complete solution of the globules.

The matrix was shown to be of a different substance from the globules. It appears to be more like the cytoplasm in composition. Unlike the globules it requires no special fixative for its preservation. At least a portion of it is insoluble in alcohol and lipid solvents such as carbon tetrachloride, for it sometimes remains intact after the use of these reagents. It is not refractive, for this character can be seen in young tissue and in injured cells to be a property of the globules only. Nor is it stained to any extent by the "fat" dyes such as Sudan III, etc. This is evident in elaioplasts with globules in Brownian movement where the stain is largely confined to the globules. That the matrix is of a plasma substance was suggested by the difficulty of staining it differentially from the protoplasm. This view was substantiated later by the identification of the elaioplasts with the plastidome and chondriome.

No evidence of a differentiated membrane about the elaioplasts could be found. None could be seen in fresh material, nor has any been brought out by reagents or fixation techniques. The only observation that might be interpreted as indicative of a membrane was the "bursting" of injured elaioplasts already described. But no fragments of membrane remained. It is more probable that the sudden freeing of the globules depended upon changes in the matrix which made it miscible with the surrounding medium.

SEASONAL VARIATIONS IN ELAIOPLASTS IN *IRIS VERSICOLOR*

Certain variations in the form and structure of the elaioplasts are due to the seasonal appearance of starch. In New England the elaioplasts are without starch from early November through June. By July or August the starch begins to appear, while by September or early October a maximum development has been reached. The disappearance of the starch then begins and proceeds rapidly. By early November no traces of it can be found.

The starch can be identified with Gram's solution and polarized light. In the former the grains stain a blue to a bluish-black, a reaction typical of starch in the presence of iodine. In polarized light they appear as bright grains with a black maltese cross on each.

The type of starch formation in rhizomes of *Iris versicolor* is characteristic and constant. Each elaioplast develops several included grains (Figs. 4b and c). Counts made in early October showed commonly from 8 to 12 grains, with a recorded range of 1 to 16 per elaioplast. Although the grains are always grouped more or less centrally within the globule-filled portion, they form bulges in the otherwise rounded contour of each elaioplast (Fig. 4). The individual starch grains are approximately isodiametric. They show the central hilum characteristic of this shape of grain when it is included within the plastid. In size they are small, generally 6 to 7 microns in diameter as measured in material collected in early October.

Climatic differences in the disappearance of the starch from the growing point of the rhizome are indicated. In material from the vicinity of Boston and of New York the starch disappears completely in the winter. But in plants grown in the Missouri Botanical Garden it may be found about the growing point in March, although completely absent from the rest of the rhizome.

The disappearance of the refractive globules of the elaioplasts has not been observed. Numerous observations have been made from September to May, during which time they remain in abundance. They are likewise present in the rhizome during June, July and August, although a less thorough study has been made of their behavior during those months.

DEVELOPMENT OF ELAIOPLASTS IN RHIZOMES OF *IRIS VERSICOLOR*

By tracing back to the meristem, the elaioplasts in the rhizome were found to develop from mitochondria-like primordia by increase in size, in visibility and in the number of contained globules (Fig. 19). In the youngest cells there are small, irregular, shadowy proplastids with two or three included non-refractive globules. In increasingly older cells

these bodies become more distinct and larger with a greater number of included globules. At the same time the globules become refractive and the whole body even more irregular in contour. Later with further increase in size and in the number of included globules, the irregular contour is lost. The cells then contain the granular, smoothly rounded, mature elaioplasts characteristic of the rhizome.

The young elaioplasts are distinguished by the following characters. They have more matrix in proportion to the number of globules than the mature forms. They do not stain after death to any degree in Sudan III nor in any other anilin dyes in contrast to the brilliant staining of the mature elaioplasts. They are restricted to a small region about the growing point, while the youngest stages are found only in the cells of the growing point. They are all irregular in contour, but this irregularity is emphasized in the intermediate forms which are almost nodulose.

The youngest stages show characters ordinarily associated with mitochondria. They are about the size of Iris mitochondria, ranging from this up to several times their size. They are indistinctly visible like much of the chondriome with a peculiar fading and reappearing quality. Thus a period of clear definition of these shadowy forms will be followed by a fading and disappearing. This, in turn, after a few minutes or after several hours may be succeeded by another period of clear definition, and so on. In general, although not always, these forms show included non-refractive globules. This is a character shared by the rod-shaped mitochondria of the species. In the young elaioplasts there is no definite arrangement of the globules which in the rod-like mitochondria always form a single row.

The formation of starch occurs in any of the young or mature forms of plastids. It was found during the season of its formation in all of them. In the young forms the starch grains ordinarily protrude from the globule-filled mass of the elaioplast, in contrast to the completely included grains of the mature elaioplast.

No evidence of increase by division was found in mature or developmental stages. No division was seen at any time, although material was collected from September to June and kept under observation for hours at a time. In the rhizome tissue even the "dumb-bell" figures so often cited as evidence of division were absent.

DEGENERATION OF ELAIOPLASTS IN RHIZOMES OF IRIS

No evidence of degeneration was found in the rhizomes of *Iris versicolor*. Elaioplasts are found unchanged and in abundance even in the oldest living cells.

Two isolated cases of degeneration of elaioplasts similar to those in *Iris versicolor* have been noted in the rhizomes of other species. One of these is an abnormal condition produced in a slowly dying plant. The second is a normal phenomenon in otherwise morphologically unchanged cells. It is apparently unassociated with the death of the cells, for no other signs of degeneration appear. This phenomenon occurs consistently in the cortex of the rhizomes and in the epidermis and sub-epidermis of the roots of *Iris macrosiphon* var. *californica*.

In *Iris macrosiphon*, elaioplasts in the mature cells of the cortex of the rhizome appear as large lipid spheres (Fig. 14c). These spheres are marked by their large size, by their distinct yellow color and by their brilliant staining in "fat" dyes, Sudan III, etc. They may be demonstrated to be in the cytoplasm by coagulating the surrounding protoplasm with fixatives (Fig. 15). The study of developmental forms which can be seen to be carried in the streaming protoplasm offers further proof of their inclusion in the cytoplasm.

Stages in the formation of the lipid spheres from mature elaioplasts can be seen in cells not far from the growing point. The process consists of the formation of homogeneous spheres by the fusion of the globules and the disintegration of the matrix (Fig. 14). A single elaioplast resolves itself into one or more of these spheres. In older cells still further fusion occurs for the spheres in them are larger and fewer. In these cells each sphere probably includes the substance of more than one elaioplast.

A similar formation of lipid spheres can be observed in epidermis and sub-epidermis of the root-tip (Fig. 18). The phenomenon is identical with that in the rhizome, although starch is present in the root elaioplasts. It shows more clearly than in the rhizome the steps in the resolution of the elaioplasts. The fusion of the globules proceeds for some time before the apparent structure of the elaioplast is lost. The final degeneration products include starch grains as well as lipid spheres. The grains and spheres remain distinct in the cytoplasm, although the starch is indiscriminately scattered among the lipid spheres.

Proof that the formation of lipid spheres in *Iris macrosiphon* is a degeneration phenomenon is based on two points. First, the structure of the elaioplast characteristic of the functioning body is lost. There is no evidence that the lipid spheres can produce starch as the elaioplasts do, or function actively in any way. Secondly, the phenomenon occurs in tissue which tends to die and slough away. In the root, the epidermal cells in which the spheres form are short-lived. This is less evident in the cortex of the rhizome where the cells may live for a season or more

after the formation of the spheres. But even in this tissue the outer cells die and the formation of lipoid spheres is more marked in the outer cells. It is not found in the inner cells of the cortex or elsewhere in the rhizome.

A second case of degeneration was found in rhizome cells of *Iris tectorum* (Fig. 7). In a slowly dying plant the elaioplasts appeared closely compacted in each cell into one or two masses. The rounded contour of each elaioplast was lost, while the matrix seemed to have become more plastic. The identity of each elaioplast was lost in the mass which appeared as a single granular body with indistinct partitions within it (Fig. 7b). Where starch was present the grains were included in the composite mass. This condition has never been found in healthy plants.

OIL-BEARING PLASTIDS IN RHIZOMES OF OTHER SPECIES OF IRIS

Oil-bearing plastids are found in the rhizomes of practically all species of *Iris*. They show the same fundamental structure and development as those in *Iris versicolor* just described. But they differ from one another in their formation of starch. Two clearly marked types based on the mode and time of starch production occur.

The first type is that found typically in *Iris versicolor* (Figs. 1, 2 and 4). It has already been described. In contrast to the second type, it is marked by the disappearance of starch during the winter dormant season, by the formation of several starch grains in each plastid and by the inclusion of the starch within the plastid. Plastids of this type vary considerably, but they usually show at least two of the general characters. In some species of *Iris* the starch persists more or less throughout the winter; in others it may persist one season and not the next, and in still others, such as *I. versicolor*, it always disappears. The inclusion of the starch in mature plastids, although not in the younger forms, is complete in most instances. But in some cases the starch grains tend to protrude slightly. This is more often the case in the cortex, although it may characterize the whole rhizome. An extreme case accompanied by an unusually reduced number of lipoid globules in the plastids (Fig. 12d) was found in one of two collections of *Iris Hartwegii*.

The second type is characterized by the persistence of the starch through the dormant season, by the formation of one, large, asymmetric starch grain or sometimes two in each plastid and by a conspicuous protrusion of the grain from the globule-filled portion of the plastid (Fig. 9). Caplike elaioplasts attached to one end or side of the large starch grains are typical of these plastids. Often the lipoid globules are larger than

in the plastids of *I. versicolor*, while the matrix is abundant enough to be clearly seen between them. A typical example of this type of plastid is found in rhizomes of *Iris pallida* (Fig. 8).

Although the disappearance of starch is not general in this second type, it has been noted in one or two instances. The starch disappears from the main part of the rhizome of *Iris pumila* during flowering (Fig. 11), although it persists around the growing point. The solution of the starch leaves peculiarly cup-shaped elaioplasts (Fig. 11c). A second case of the disappearance of starch may occur under abnormal conditions. It was induced in the rhizomes of *Iris pallida* placed in the greenhouse during the winter. It is accompanied by a lack of vigor and the disappearance from the rhizome cell vacuoles of substances ordinarily present at that season. The change in the vacuoles is apparent in fixed material in a lack of the precipitate characteristically produced in them by reagents during the winter. The plastids in the rhizomes of the greenhouse plants resembled the spherical ones of winter material of *Iris versicolor* except for their smaller size and fewer numbers.

The distribution within the genus of the two types of rhizome plastids has been found to follow closely the recognized taxonomic grouping. The homogeneous and closely related groups show the same type of plastid, while a heterogeneous group such as the Apogon shows both types. In the latter case aberrancies from the prevailing type in the group are often correlated with anomalous taxonomic characters. Sufficient material has been examined to show definitely the condition in the two largest groups, Pogoniris and Apogon, and in several of the smaller groups, Evansia, Regelia and the Pardanthopsis and Gynandiris species. An indication of the prevailing type in each of the other groups may be found in the notes made on a few representative species.

Rhizomes have been examined largely during the late winter. In late winter the pallida type of plastid shows its characters clearly, while the versicolor type is generally without starch at that season. An indication of the mode of starch formation in the latter type of species can often be obtained from the persistent starch in the plastids about the growing point. In this study, such observations have been supplemented by notes made during the starch-forming season.

The pallida type of rhizome plastid occurs characteristically in Pogoniris, Regelia and Oncocyclus. These are homogeneous groups which together with Pseudoregelia form a unit of closely related species. The same type has been found in a Juno Iris and in a Xyphium Iris. In the latter case it occurs only in tissue about the vascular bundles but not in the large parenchyma cells which are filled with starch. It is also found

in *Pardanthopsis*, in the closely related hexagona sub-group of the Apogons, in the anomalous Apogon, *I. verna*, and in one of the variable Apogon spuria group, *I. spuria ochroleuca*.

The versicolor type of plastid appears in the Evansia group and in the majority of the Apogons. In the latter it characterizes the following sub-groups: *Sibirica*, *Laevigata*, *Longipetala*, *Californian*, *Tripetalous*, *Spuria* and *Ensata*. Its distribution is more limited than that of the pallida type, for the Evansia and Apogon sub-groups include but one-third of the species. The pallida type appears to characterize the other two-thirds of the genus. Since the Evansia and Apogon sections include all of the American irises, the versicolor type is predominantly the type found in North American species. The only exceptions are the anomalous Apogons cited in the preceding paragraph and one to be described later. A similar predominance of the versicolor type is to be found in the Asiatic species. The American and Asiatic species contrast in this respect with the more strictly European and Mediterranean species, which belong chiefly to groups showing a pallida type of plastid, notably Pogoniris and related groups and the bulbous forms.

The absence of oil-bearing plastids has been noted in five irises. In these cases the rhizome cells are filled with starch. The starch is of two types paralleling in distinguishing characters and in distribution the two kinds formed by the oil-bearing plastids. One is present as large, single, asymmetrical grains similar to those in the pallida type of oil-bearing plastid. They characterize the anomalous Apogon, *Iris unguicularis*, the Reticulata Iris and Gynandiris. The last of these is not always included in the genus; in the formation of starch and no lipoid in its corms it resembles the closely related genus, *Moraea*. The Reticulata is a group closely related to the Xyphium, which shows similar starch grains and a few oil-bearing plastids of the pallida type. The second starch grain type resembles the starch grains of the versicolor plastids in their small size, in their isodiametric shape and in their formation in groups within a single leucoplast. Like the versicolor type of plastid they are found in Apogon Irises, the Japanese Iris and *Iris Sinitensis*. The former is a hybrid of *I. laevigata*, one of a group characterized by the versicolor type of plastid, and another member of the same group. The other *Iris* belongs to the Spuria sub-section, a group of intergrading and variable forms, for which no single characteristic type of plastid was found.

For the type of plastid found in individual species, the reader is referred to the table on page 246 and also Figs. 12 and 13. The table also includes data on the material, its source, the season of examination, etc.

TABLE OF IRISES EXAMINED SHOWING THE TYPE OF RHIZOME PLASTID AND THE SOURCE OF THE MATERIAL FOR EACH SPECIES!

SPECIES	SECTION	GROUP	TYPE	SOURCE OF MATERIAL	PARTS	SEASON COLLECTED	SEE PL. 133, FIG. 13
<i>I. pallida</i> Lam. X?	Pogoniris	Pallida	2	Bussey Garden	All	All	Qa
<i>I. pallida</i> variety	Pogoniris	Pallida	2	Mo. Bot. Gard.	r, l	March	Qf
<i>I. cuneollii</i> Amb.	Pogoniris	Pallida	2	Mo. Bot. Gard.	r, l	March	Qe
<i>I. pumila</i> L.	Pogoniris	Pumila	2	Mo. Bot. Gard.	r, l	March	Pb
<i>I. pumila</i> variety	Pogoniris	Pumila	2	Mo. Bot. Gard.	r	April	Pa
<i>I. Korolkovi</i> Regel	Regelia	Regelia	2	Brooklyn Gard.	r	April	O
<i>I. Hoogiana</i> Dykes	Regelia	Regelia	2	Brooklyn Gard.	r	April	N
<i>I. susiana</i> L.	Oncocylus	Oncocylus	2	Mo. Bot. Gard.	r, l	March	M
X <i>I. "Zwaenenburg"</i> Hort.	Juno	Juno	2	Brooklyn Gard.	bulb	April	R
<i>I. alata</i> Poir.	Xyphium	Xyphium	2	{ Florist	f, l	Feb.	Ia
<i>I. Xyphium</i> L.	Pardanthopsis	Hexagona	2	{ Mo. Bot. Gard.	bulb	March	—
<i>I. dicholoma</i> Pall.	Apogon	Hexagona	2	Mo. Bot. Gard.	r, l	March	Ic
<i>I. foliosa</i> Mack. & Bush	Apogon	Hexagona	2	{ Mo. Bot. Gard.	r, l	March	—
<i>I. fulva</i> Ker	Apogon	Hexagona	2	Brooklyn Gard.	r	April	—
X <i>I. hexagona</i> Walt. X?	Apogon	Hexagona	2	Mo. Bot. Gard.	r, l	March	Ib
<i>I. vinicolor</i> Small	Apogon	Hexagona	2	Brooklyn Gard.	r	April	H
<i>I. verna</i> L.	Apogon	Verna	2	Virginia	r	May	Ee
<i>I. spuria</i> Pall. var. <i>ochroleuca</i>	Apogon	Spuria	2	Mo. Bot. Gard.	r, l	March	Ea
<i>I. halophila</i> Pall.	Apogon	Spuria	1	Brooklyn Gard.	r	April	C
<i>I. ensata</i> Thunb.	Apogon	Ensata	1	Brooklyn Gard.	r	April	Fb
<i>I. setosa</i> Pall.	Apogon	Tripetalous	1	Brooklyn Gard.	r	April	Fa
<i>I. setosa</i> var. <i>canadensis</i> Foster	Apogon	Tripetalous	1	Brooklyn Gard.	r	April	Da
<i>I. Douglasiana</i> Herb.	Apogon	Californian	1	{ Brooklyn Gard.	r	April	—
<i>I. Hartwegii</i> Baker	Apogon	Californian	1	{ California	r, l, o	Aug.	—
<i>I. macrosiphon</i> Torr. var.	Apogon	Californian	1	{ California	r, l, o	Aug.	Dc
<i>I. tenax</i> Dougl.	Apogon	Californian	1	Brooklyn Gard.	r	April	Db
<i>I. longipetala</i> Herb.	Apogon	Longipetala	1	Brooklyn Gard.	r	April	—
<i>I. missouriensis</i> Nutt.	Apogon	Longipetala	1	California	r	Sept. July	—

TABLE (Continued)

SPECIES	SECTION	GROUP	TYPE	SOURCE OF MATERIAL	PARTS	SEASON COLLECTED	SEE PL. 133, FIG. 13
<i>I. virginica</i> L.	Apogon	Laevigata	1	Mo. Bot. Gard.	r, l	March	Bb
<i>I. versicolor</i> L.	Apogon	Laevigata	1	{ Mo. Bot. Gard. Boston	r, l All	March All	Ba
× <i>I. robusta</i> E. Anders.	Apogon	Laevigata	1	Mo. Bot. Gard.	r, l	March	—
<i>I. pseudacorus</i> L.	Apogon	Laevigata	1	{ Bussey garden Arnold Arbor.	r r	—	Bc
<i>I. Kaempferi</i> Sieb.	Apogon	Laevigata	1	{ Mo. Bot. Gard. Brooklyn Gard.	r, l r	March April	—
× <i>I. Wilsoni</i> Wright ×?	Apogon	Sibirica	1	Brooklyn Gard.	r	April	Bd
<i>I. sibirica</i> L.	Apogon	Sibirica	1	Mo. Bot. Gard.	r, l	March	Ad
<i>I. prismatica</i> Pursh	Apogon	Sibirica	1	{ Duxbury, Mass. { N. Y. Bot. Gard.	r, l r	—	Aa
<i>I. orientalis</i> Mill.	Apogon	Sibirica	1	Brooklyn Gard.	r	April	Ae
× <i>I. "Questi"</i> Hort.	Apogon	Sibirica	1	Mo. Bot. Gard.	r, l	March	Ac
<i>I. Clarkei</i> Baker	Apogon	Sibirica	1	Mo. Bot. Gard.	r, l	March	—
<i>I. chrysographes</i> Dykes	Apogon	Sibirica	1	Brooklyn Gard.	r	April	Ab
<i>I. cristata</i> Ait.	Evansia		1	{ N. Carolina { Mo. Bot. Gard.	r r, l	May March	—
<i>I. gracilipes</i> A. Gray	Evansia		1	{ N. Y. Bot. Gard. { N. Y. Bot. Gard.	r r	April April	Ja
<i>I. tectorum</i> Maxim.	Evansia		1	{ Mo. Bot. Gard. Brooklyn Gard.	r, l r	March April	Jb
<i>I. lacustris</i> Nutt.	Evansia		1	Brooklyn Gard.	r	March	Jc
<i>I. japonica</i> Thunb.	Evansia		1	Brooklyn Gard.	r	April	Je
<i>I. angusticularis</i> Poir.	Apogon		3	Brooklyn Gard.	r	April	Jd
<i>I. reticulata</i> Bieb.	Reticulata		3	Brooklyn Gard.	r	April	G
<i>I. sibiricum</i> L.	Gynandris		3	{ N. Y. Bot. Gard. Brooklyn Gard.	bulb corn	April	L
<i>I. Sintensis</i> Janka	Apogon	Spuria	4	Brooklyn Gard.	r	April	K
<i>I. laevigata</i> Fisch. ×?	Apogon	Laevigata	4	Mo. Bot. Gard.	r	March	Eb
							Be

1—versicolor type of rhizome plastid

2—paluda type of rhizome plastid

3—rhizome plastid with single large starch grain and no oil

4—rhizome plastid with several small starch grains and no oil

r—rhizome, l—leaf, f—flower, o—root

1 Nomenclature according to Dykes, The Genus Iris.

OIL-BEARING PLASTIDS IN RHIZOMES, BULBS ETC. OF OTHER PLANTS

No oil-bearing plastids have been found in any other rhizomes or bulbs examined. None are present in either of the species of *Moraea* examined, a closely related genus replacing *Iris* in the southern hemisphere. Nor are there any in the many Araceae, Bromeliaceae, Commelinaceae, Liliaceae and Scitamineae examined. Rather, all of these plants contain large asymmetric starch grains in their storage organs.

The chloroplasts in all of these plants characteristically contain more or less refractive granules. In general, such appears to be the condition in all of the monocotyledons and in many of the dicotyledons. Indeed it seems to be true even of some of the lower forms such as the liverworts and mosses, although in these the granules are often not refractive.

The following is a list of the species of monocotyledons examined. The species are grouped according to families.

ARACEAE: *Acorus Calamus* L., *Aglaonema* sp., *Arisaema triphyllum* (L.) Schott, *Dieffenbachia* sp., *Nepenthes* sp., *Philodendron Selloum* C. Koch, *Philodendron cordatum* Kunth, *Schismatoglottis crispata* Hook. f., *Schismatoglottis rupestris* Zoll. and Mor., *Spathiphyllum* sp.

BROMELIACEAE: *Ananas macrodentes* E. Morr., *Billbergia* sp., *Cryptanthus* sp.

COMMELINACEAE: *Palisota* sp.

IRIDACEAE: *Moraea iridioides* L., *Moraea* sp.

LILIACEAE: *Allium* sp., *Heisteria* sp., *Ornithogalum umbellatum* L., *Yucca filamentosa* L.

ORCHIDACEAE: *Vanilla planifolia* Andr., *Vanilla pompona* Schiede.

MUSACEAE: *Strelitzia* sp.

ZINGIBERACEAE: *Alpinia nutans* Rosc., *Amonum* sp., *Hedychium* sp.

MARANTACEAE: *Calathea* sp.

OIL-BEARING PLASTIDS IN OTHER PARTS OF THE PLANT OF IRIS SPECIES

The observations in this section apply to any species of *Iris* unless otherwise stated. A careful study has been made of the conditions in *Iris pallida* and in *Iris versicolor*. Additional notes have been made on other species.

The formation of oil globules is characteristic of plastids throughout the tissues of plants of the genus *Iris*. The globules are not always so numerous as those in the rhizome plastids of *Iris versicolor* where they are developed to an unusual degree. An extreme example of a limited formation of globules is found in the chloroplasts of the guard cells where

the matrix of the plastids is relatively abundant and clearly visible. Nor are the lipoid globules usually the only observable product of the plastids. Ordinarily starch is also present, while in some plastids chlorophyll or a yellow pigment is formed.

The elaioplast condition described for rhizome plastids of the versicolor type may occur in any of the uncolored tissues. It is dependent upon the absence of starch and pigment and upon a large production of oil. Such conditions are found at times in the rhizome, in the root and in uncolored leaf and flower tissues.

In the rhizome and root elaioplasts occur generally throughout the tissues of these organs. They are restricted to certain species and, at least for the rhizome, to certain seasons. There is no connection between their presence in the rhizome of a species and their appearance in the root of the same species. For example elaioplasts were found in the rhizome of *Iris versicolor* but not in the root (Figs. 2 and 35). On the other hand, they were found in the root of *Iris pallida* but not normally in the rhizome (Figs. 9 and 30). An example of their formation as a seasonal phase of the leucoplasts in the rhizome has already been described for *Iris versicolor*. Whether or not they also form a seasonal phase for leucoplasts in the root has not been investigated.

In the leaf and flower the elaioplasts are restricted to a few cells. Often they are but transitional forms appearing for a very brief time. Such is the case in the flower where they may occur in the course of the development of the chromatophores. Because of their limited occurrence in a few cells it is usually easy to identify them with the leucoplasts or chromatophores in neighboring cells. In these tissues they do not develop the brownish color so characteristic of the rhizome elaioplasts in *Iris versicolor*. Instead they remain entirely colorless.

The development of elaioplasts can be induced under unfavorable conditions. An example of this has already been cited in their formation in rhizomes of *Iris pallida* grown in the greenhouse (p. 244). In this case they were formed by the dissolution of the starch leaving only the oil-bearing plastid. By growing plants in semi-darkness chloroplasts can be prevented from forming pigment or starch. They then appear as elaioplasts. In neither of these cases is an increase in the number of oil globules involved. Nor has the formation of unusual numbers of elaioplasts been observed as a result of abnormal conditions.

The oil-bearing plastids in other parts of the plant show essentially the same features as those described for the rhizome. They differ from those in the rhizome in minor characters, also in the absence of a general elaioplast phase except in the root and in the formation of pigments. In

addition they show in some cases chondriome types as an intermediate stage in their development from the proplastids. In some tissues, notably in the flower and in epidermal tissues, the mature plastids often show further changes involving chondriome types not found in the rhizome. These points will be taken up separately in the succeeding paragraphs.

Minor differences between the plastids in other parts of the plant and the type found in the rhizome and root appear in the lesser production of lipoid globules and in their complete lack of color in colorless tissue. Correlated with the smaller number of globules is a greater stability. This is shown in their greater resistance to injury by mechanical pressure and to distortion or destruction by reagents. Their lack of color when not pigmented can be seen in colorless leaf tissue in marked contrast to the strongly yellowish cast in the equally unpigmented rhizome plastids. This is particularly well shown in *Iris versicolor*.

The formation of pigment, chlorophyll or yellow pigment, occurs ordinarily in the young plastids. But there is no specific stage at which it is developed. In the leaf chloroplasts it often forms shortly after the appearance of starch in the young plastids, although it may not develop for some time. In the chromatophores of the root it sometimes appears before the formation of starch, for example in the rootcap of *Iris versicolor*. At other times yellow pigment appears in plastids which do not form starch, for example in the chromatophores of roots of *Iris pallida*. In many cases yellow pigment is found in chondriocent types of plastids, but its formation is quite unconnected with the phenomena producing these forms. Proof of this is found in its formation in the approximately spherical plastids of the root-tip before they pass into a chondriocent state and in those of the rootcap of *Iris versicolor* where the mature plastids retain a more or less spherical state.

The location of pigment in the refractive globules and also in the matrix and its greater solubility in the former was demonstrated. In the guard cells of *Iris pallida*, where there is little chlorophyll, the green color can be seen to be confined to the globules, while the matrix remains colorless. That it may also be dissolved in the matrix is shown in degenerating chromatophores of the root where color remains in the matrix after the disappearance of the refractive globules.

Intermediate developmental forms of the plastids are found in the root-tip (Figs. 20-24). They differ from the small plastids in other differentiating tissue by the retention for a longer period of the shadowy visibility of the proplastids and by a plasticity amounting in the younger stages to an almost fluid character. They resemble other young plastids

in their origin in the proplastids, in their development by increase in size, in visibility, in the number of included globules and in their final development in many cells into the same type of plastid. In their often elongated shape they resemble the chondriocots of many authors.

The shadowy character of the younger intermediate forms is evident in the peculiar fading and reappearing already described for the proplastids (p. 241). With the differentiation of the tissue this shadowy quality is lost (Figs. 20-24), but the bodies do not become refractive until a late stage (Figs. 24 and 25). Often the more or less indistinct forms persist for long periods.

The plastic quality of the intermediate forms is shown in their more or less elongated shape and in their movement in the streaming protoplasm. The movement consists of a continuous changing of form (Figs. 20-23). Both movement and elongation are more marked in the younger stages, some of which are almost fluid. In older cells the plastids become less and less elongated with increasing viscosity until they are more or less spindle- or tadpole-shaped. At the same time the motion of the plastid becomes reduced to a moving about of the ends. In the fully differentiated plastid the shape is roughly spherical and there is no movement. Often the plastids remain in the spindle- or tadpole-stage for some time.

The continuous motion of the intermediate types is essentially an amoeboid movement of the plastid (Figs. 20-23). This appears to some degree in all of the intermediate types. In its most exaggerated expression in the youngest stages, it consists of a change in form from a filament, through intermediate stages, to a sphere. Another example characteristic of the plastids before the globules have become refractive is the formation of two swollen ends connected by a thread. In some cases the thread becomes invisible, but it always reappears and shortens to reunite the two ends. In its least pronounced form in the older spindle- and tadpole-shaped forms, the movement is confined to a turning from one side to another of the tapered ends.

That the movement is not wholly connected with cyclosis, although probably aggravated by it, appears likely. In cells where there is no cyclosis, the intermediate forms customarily show a pulsating movement associated with changes in thickness. An example of this is seen in young plastids in the isodiametric cells of the rootcap.

It is worthy of note that in none of these forms has division of the plastids been seen. Many observations have been made at different times and over periods of an hour or more. But even plastids which appear to be divided are seen shortly to be connected by a thread which after a time thickens to reunite the two parts.

The liquid character of the youngest forms is shown in the movement of the globules within the plastid. This consists of a sloshing about of the globules. In older forms this movement does not appear. Any rearrangement of the globules in them is due to the amoeboid movements of the plastid.

The intermediate plastid types develop into leucoplasts in the cortex of the root or into chromatophores in the rootcap. But in other regions of the root and in the elongated cells of the fibrovascular bundles throughout the plant they persist as chondriocont types. The shadowy, very plastic forms are found in the central cells of the root. In other parts of the central cylinder more differentiated forms are found. Similar ones appear in the fibrovascular bundles throughout the plant. In the inner cortex the tadpole- and spindle-shaped forms with refractive globules often remain. The chromatophores of the rootcap often retain their chondriocont-like shape and plasticity after the formation of pigment and oil (Fig. 29b).

Associated with the persistent developmental forms are shadowy leucoplasts and mitochondrial types not ordinarily linked with plastids. In *Iris*, the latter are marked by their gradation into the plastid forms. In the same cells with the persistent chondriome-like plastids, they appear as long filaments with a single row of globules and a twisting or wavy motion in the streaming protoplasm (Figs. 26-27). Some of the filaments are shadowy, while the granules in others are refractive. The filaments with refractive granules sometimes show thickened ends which contain more than one row of granules.

It may be noted here that in addition to the proplastids and filamentous chondriosomes, the more usual types of mitochondria, that is globular or rod-shaped forms, are found in *Iris*. They appear in all cells but are concentrated about the apical meristems and in tissues of the leaf and root. They are less evident in the cells of the rhizome. Two observations are worth recording. The so-called spherical mitochondria were observed to be more or less fluctuating in form and only approximately spherical. The rod-shaped ones were seen to contain globules.

Changes in plastids after "maturity" are found in epidermal cells and in the flower. The changes in both cases are marked by an increasing fluidity of the matrix and by the disappearance of the refractive globules. In the epidermis of the root and in the flower the changes culminate in the death of the cell. But in the leaf epidermis the plastids remain as more or less shadowy chondrioconts (Fig. 37). These are quite similar in appearance and in motion to the developmental types in the root.

The changes in the plastids in the epidermal cells of the root have

been carefully studied. The more or less spherical leucoplasts or chromatophores first become somewhat elongated (Fig. 31). This is followed in older cells by increasing fluidity of the matrix and the gradual disappearance of refractive globules (Figs. 31-33). Where the plastids are pigmented some of the pigment remains after the globules are gone, but this also tends to disappear. Where these changes progress far, the plastids become shadowy nets much elongated in shape (Fig. 33). In the streaming protoplasm, they are often partially drawn out into long filaments (Fig. 32). In some cases the attenuated portions are bent back upon the rest of the plastid so as to include a small amount of protoplasm (Figs. 30, 33, 34). When an oil globule is included with protoplasm it is often in Brownian movement. The attenuated forms persist until the death of the cell.

During flowering the leucoplasts of the floral tissue were seen to undergo a series of changes similar to those described as occurring in the root. These have not been studied in detail, but the following general changes have been noted. The leucoplasts become pigmented and chondriocont-like in shape. As the flower opens and fades the chromatophores become more and more fluid. At the same time the refractive globules disappear. An advanced stage shows them partially drawn out into long filaments (Fig. 34). Unlike the chromatophores of the root the pigment is retained. These forms remain until the death of the cell. Similar changes occur in the leucoplasts of the bracts.

In *Iris Xyphium* the formation of refractive bosses on the pollen grains from oil-bearing chromatophores has been demonstrated (Fig. 17). In unripened anthers the pollen shows no markings except the small refractive dots forming a part of the wall structure. The grains are surrounded by the tapetal fluid in which are numerous oil-bearing chromatophores. In the shed pollen the grains show not only the refractive dots but the closely appressed chromatophores which appear as granular, yellowish, refractive bosses. No similar observations have been made on pollen grains of other species. Although the latter show refractive spines or a network of refractive structures, these are in every case associated with wall formation. They are in no way connected with the plastidome or chondriome.

All of the plastids described are found to show the following general characters. They tend to aggregate about the nucleus, a character also shown by mitochondria. Unless degeneration is involved they retain the ability of the proplastids to form the pigments and other products differentiating the different types of plastids. They also retain the ability to change from the plastid shape into a chondriocont form and *vice versa*.

ELAIOPLASTS IN PLANTS DESCRIBED IN THE LITERATURE

Of the plants recorded in the literature as forming elaioplasts the following have been examined: *Vanilla planifolia* Andr., *V. Pompona* Schiede., *Marchantia polymorpha* L., *Lunularia cruciata* (L.) Dum., *Pellia epiphylla* (L.) Corda, *Porella* sp., *Bazzania trilobata* (L.) S. F. Gray, *Scapania nemorosa* (L.) Dum., *Cephalozia* sp., *Trichocolea tomentella* (Ehrh.) Dum., *Plagiochila asplenioides* (L.) Dum., *Lophocolea heterophylla* (Schr.) Dum., two thallose species of the Jungermanniales from Oregon and two leafy species of the Jungermanniales from Oregon.

The two classes of elaioplasts described by Pfeffer, Wakker and later writers were examined. These are the oil bodies characterizing the liverworts and those in *Vanilla*, a classical example of elaioplast-bearing monocotyledons. In both cases certain of the observations of previous writers have been verified and some additional notes made.

The following observations made by earlier writers for *Vanilla* have been verified. The elaioplasts are present as highly refractive granular bodies near the nucleus in cells which contain also leucoplasts and chloroplasts. Structurally they consist of globules of refractive oil in a protein or plasma matrix. They are marked by their brilliant staining in "fat" dyes and by the extrusion of large globules of oil after treatment with various reagents.

In addition it has been noted that the elaioplasts are generally distributed in all the cells of leaf, stem and root tissues rather than restricted to particular tissues in certain parts of the plants.

It has also been observed that the single large elaioplasts are aggregates of smaller granular bodies (Fig. 45). The aggregation is more or less compact. In some cells it is difficult to distinguish the individual bodies, while in other cells they are but loosely grouped or freely circulating in the streaming cytoplasm (Fig. 46). In some cells the smaller bodies could be observed to aggregate into one or more groups from which individuals were carried away from time to time by the streaming protoplasm.

The development of the smaller bodies from non-refractive granular ones can be observed in younger cells of leaf and root. In successively older cells the included globules gradually become more and more refractive until the bodies assume the highly refractive condition typical of mature cells. In the less refractive stages the bodies seldom form compact aggregations. No specific stage has been noted in which aggregation becomes the rule. The formation of compact groups appears possible at any time, although more characteristic of mature tissue.

The rotary movement of elaioplasts described by Zimmermann and others as characteristic of these bodies has been shown to be an injury phenomenon. It is observed in cells which soon show unmistakable signs of injury followed by death. It is not seen in any cells which remain normal in appearance and actively streaming for a period of hours. The movement consists of rotation within a liquid vacuole. It is followed by Brownian movement of cytoplasmic inclusions and a general coagulation or disintegration of the cellular structure, that is by unmistakable signs of death.

In the liverworts the following observations of earlier writers have been verified. Bodies included within the cytoplasm and marked by their refractivity, by their staining in "fat" dyes and by their solubility in alcohol appear generally throughout the group. They are located within the ring of chloroplasts, but, unlike those in *Vanilla*, show no particular affinity for the nucleus. They all characteristically leave a residual ring in solution with alcohol, etc. They vary in color from colorless to dark brown. Two or three classes are distinguishable. The first appears as a single large granular mass almost filling the cell lumen (Fig. 38). It is located in scattered cells throughout the plant body and is characteristic of the Marchantiales. The second and third types are found in the Jungermanniales which they characterize. They are smaller than those in the Marchantiales and are round, spindle- or disc-shaped in form (Figs. 40-44). They grade from a homogeneous type to a very granular one. Commonly there are from one to twenty in a single cell, located more or less characteristically in the peripheral cytoplasm. In this group they are not restricted to particular cells but are found in every cell. Unlike the bodies in *Vanilla* there is little or no tendency for them to aggregate.

The development of the bodies has been observed in the Jungermanniales (Fig. 42). In the younger cells the oil-bodies appear as shadowy, wrinkled, granular bodies. They develop into the mature bodies of older cells by an increase in substance and in the refractivity of the granules. By the time the cells are fully mature, the bodies have become plump and refractive. There is no indication of a vacuolar origin postulated by some writers.

In addition the following new observations were made. The homogeneous type found in the Jungermanniales are sometimes seen with attached granular bodies (Fig. 44). These appear in the younger cells.

The single bodies in the Marchantiales can be shown to be aggregations of smaller ones. This is apparent in younger cells where they are less refractive and less highly colored (Fig. 39). In older cells the

structure is obscured by the dark color. Likewise in older cells the bodies appear to be more closely compacted.

The Brownian movement described by some as characteristic of the bodies in certain species has been shown to be associated with older bodies or with injury. It is never seen in younger tissue, even in cells with mature oil bodies. It appears in some of the older cells of the Marchantiaceae and can be induced in any cell by injury.

DISCUSSION

It has been shown in the preceding observations that the oil bodies in *Iris* are a phase of ordinary plastids. In studying the development and variations of these plastids, many interesting observations have been made which have a bearing upon the status of elaioplasts and upon various problems concerning plastids. In particular the observations provide further evidence of the plastid character of elaioplasts and of a relationship between the various types of oil bodies described in the literature. They also clarify our conception of the interrelationships of plastids and chondriosomes.

1. SIGNIFICANCE OF PRESENT STUDY IN THE INTERPRETATION OF ELAIOPLASTS

To identify the anomalous bodies in *Iris* as a seasonal elaioplast phase of plastids adds another instance to the accumulating evidence of the plastid character of oil bodies. This substantiates the theories of Wakker (47), of Beer (4), of Hieronymus (22) and of Kozlowsky (28) who postulate a relationship with plastids rather than with vacuoles or with the nucleus. There is no evidence in any of the observations described in this paper of a vacuolar origin or identity. On the contrary, the structural, developmental and chemical similarities between vacuoles and oil bodies recorded by some authors were not observed in any of the material examined. Nor was there any evidence of a nuclear derivation of the elaioplasts, a theory based upon the similarity in the staining properties of the nucleolus and elaioplasts and in the aggregation of the elaioplasts about the nucleus. Both of these phenomena have been found to be characteristic of plastids in general. The possibility remains that some elaioplasts may be more or less fused aggregations of oil globules which bear no relationship to plastids. The phenomenon was not observed, but the possibility of its occurrence was not disproved.

It is probable that the granular elaioplasts of the monocotyledons and liverworts are types of plastids. They show the same structure as

that of the plastids, that is a matrix with embedded globules. That the stroma in the liverworts is non-fixable is not significant morphologically, although it indicates a chemical difference between the oil bodies in the liverworts and plastids in general. Further evidence of the plastid character of the granular oil bodies in the monocotyledons is found in their similarity in appearance and in general characters to those found in *Iris*. A comparison between the elaioplasts in *Vanilla*, as a classic example of the type found in monocotyledons, and those in *Iris* shows the following characters common to both: presence of refractive granules, brilliant staining in "fat" dyes, extrusion of oil with picric acid, etc., aggregation about the nucleus, yellowish color, plastid structure and the absence of the more usual plastid products such as starch and pigment.

That the homogeneous oil bodies in the liverworts may be classed like the granular types as plastids is suggested. Heretofore no distinction has been made between the two types because of the intergradation occurring between the two extremes. The appearance of attached granular portions in the younger stages of the homogeneous forms substantiates the view that they should be classed with the granular types which, as has been suggested, are plastids.

That elaioplasts are sometimes a phase of functional plastids as well as degenerate forms has been brought out in these studies. Heretofore they have been considered to be degenerate forms or secretions of plastids. In *Iris* they are found as functional plastids, as evidenced in the formation of starch and their apparently continuous presence in individual cells from season to season. That elaioplasts sometimes form by degeneration of plastids involving the production of oil has been shown by Beer (4). There is no evidence that they are ever secretions from plastids.

It is probable that the granular elaioplasts described in the literature are sometimes functional plastids and sometimes degenerate forms. Those found in such organs as leaves, roots and bulbs or those found widely distributed throughout the plant as is the case in *Vanilla* are doubtless active plastids, while those restricted to the more or less evanescent floral tissues are probably degenerate plastids.

The interpretation of the homogeneous oil bodies in the liverworts is not clear. They might be degeneration products, but they might also be an accumulation of normal plastid products within a plastid.

It has also been shown in the studies of *Iris macrosiphon* that elaioplasts of the type described by Lidforss (32) as homogeneous oily spheres may form by the degeneration of oil-bearing plastids. A similar

phenomenon has been described by Beer (4) as a final step in the degeneration of plastids in floral tissue of *Gaillardia*. That the spheres described by Lidforss (32) are likewise degeneration products of plastids can only be surmised. It is possible that they are more or less fused aggregations of oil globules unconnected with plastids.

Evidence of a relationship between the various types of elaioplasts described in the literature has been found in these studies. A structural similarity is seen between the oil bodies in the Marchantiaceae and those in *Vanilla* in that they are both aggregations of plastid-like bodies. I have found no record in the literature of the aggregation of these bodies in the Marchantiaceae, although the phenomenon was noted for elaioplasts in the monocotyledons as early as 1914. In addition to this direct evidence of structural similarity the observations upon the development and variations of elaioplasts in *Iris* have demonstrated that these oily plastids show, at one time or another, the widely varying phenomena which have heretofore been considered distinctive of different types of oil bodies. It has already been pointed out that elaioplasts of the homogeneous type described by Lidforss (32) sometimes result as a degeneration product of a granular type of elaioplast. It has also been found in *Iris* that the oily plastids show at one time or another the following phenomena described in the literature for oil bodies: aggregation and fusion of homogeneous oil globules, aggregation and compacting of plastid-like bodies, aggregation about the nucleus, unrestricted position in the cell, degeneration involving the disappearance of the oil and degeneration involving the formation of oily spheres. In brief the morphological distinctions between the various classes of oil bodies appear to be breaking down, while it is evident that plastids can show widely varying phenomena which, considered separately, might be interpreted as bases for the distinction of fundamentally different types. Further study on this subject is highly desirable. In particular further observations on oil bodies and plastids in *Vanilla*, *Ornithogalum* and the hepatics are needed, for much of the literature deals with elaioplasts found in them.

An additional point which tends to reduce the number of recorded distinctions between the oil bodies in the liverworts and those in the monocotyledons appears in the permanent character of the elaioplasts in the rhizomes of *Iris*. Heretofore elaioplasts in monocotyledons have been described as temporary structures, while those in the hepatics have been thought to be more permanent. It may be noted here that my own limited studies made on *Vanilla* indicate that elaioplasts are not the temporary structures even in this classical plant that one would infer from the literature.

That conditions producing oil bodies are more or less restricted in their occurrence in the monocotyledons has again been brought out in these studies. Elaioplasts do not appear generally throughout the group, although the appearance of oil-bearing chloroplasts is not uncommon. This study adds another genus and many species to the published lists of monocotyledons in which elaioplasts occur. Although oil-bearing plastids occur in the rhizomes of practically all species, it is noteworthy that the elaioplast condition is restricted for the most part to the *Apogon* irises of Asia and America. This is the first record that I find of the occurrence of oil bodies in rhizomes, although Politis (39) has described them in bulbs.

Evidence of the function and significance of the oil bodies has been found. In *Iris* the bodies are clearly assimilative organs as shown by their formation of starch. That the oil itself is a reserve food supply is indicated. In certain species it replaces at least morphologically the starch stored in the rhizomes of other species. There is no evidence that the elaioplasts are ever excretions, although they may be at times degeneration products.

There is no evidence of the division of elaioplasts recorded by a few writers. The fragmentation described by Raciborski (41) and Politis (39) is but the separating of the aggregated plastid-like bodies. This can be seen in *Vanilla*. That there is ever a passive division of an aggregated mass of oil bodies by the cell wall is improbable. Neither such aggregations nor a great development of oil was found in the meristems of *Iris*, *Vanilla* and the hepatics.

2. SIGNIFICANCE OF PRESENT STUDY IN INTERPRETATION OF PLASTIDS AND CHONDRIOSOMES

With the recognition of elaioplasts as plastids, a study of their variations became a study of the variations in plastids and chondriosomes. No new phenomena have been noted, but significant interpretations of those already recorded in the literature¹ have been made.

Most striking of the phenomena observed was the development of large quantities of oil globules in plastids. The formation of oil globules in plastids has been known for a long time and has recently been emphasized by Guilliermond's (15-20) studies of *Iris*. But even Guilliermond's extensive investigations have not shown an accumulation of oil in plastids comparable to that found in *Iris versicolor* where the quantity is

¹A summary of the present status of plastids and chondriosomes may be found in books and papers by Schürhoff (44), Sharp (45), Guilliermond et al. (20) and Mottier (37).

so great as to obscure the structure of the plastids and render them unrecognizable for months at a time.

The association of oil globules with young or degenerating forms more frequently than with mature plastids has been suggested by Guilliermond et al. (20). But such is not the case in *Iris* where the largest formation of oil is in the functioning plastids of the rhizomes.

A second phenomenon noted was the plastic quality of chondriosomes and of transitional types of plastids. As evidenced in amoeboid movements this has often been recorded in the literature, while it has been emphasized in the recent studies by Guilliermond and his associates. But I have found in the literature no reference to the extreme plasticity amounting to fluidity such as occurs in some young leucoplasts where the included globules are moved about at random within the plastid.

The significance of the chondrioconts has been brought out clearly in the survey of the variations of plastids and chondriosomes made in this study. The chondrioconts are essentially plastids producing at times all of the visible products of plastids such as starch, chlorophyll or a yellow pigment. They share, too, the plastic qualities of plastids which they display to a much greater degree. They occur in restricted tissues as transitional stages in the formation of plastids from mitochondria-like primordia or as more or less degenerating forms of plastids. Often in the rootcap and in floral tissue they are pigmented, although the formation of pigment is not confined to them. It should be noted that in some tissues chondrioconts persist without assuming the more usual plastid form.

Chondrioconts should not be interpreted as invariably forming a stage in the development of chloroplasts [Guilliermond et al. (20)]. On the contrary my studies show that the majority of chloroplasts and other plastids develop from mitochondria-like primordia without the intervention of a chondriocont stage. Where chondrioconts do form a stage in the development of plastids, the whole chondriocont develops into a plastid. There is no budding or fragmenting of the chondriocont involved. The appearances that have been interpreted as budding in chondrioconts or as evidence of fragmentation are but temporary shapes of the plastic chondrioconts.

It may be noted here that the studies of chondrioconts emphasize Kassmann's (25) observations that plastids do not divide under normal conditions. This is a much debated point in the literature upon plastids.

There was no evidence of vacuole formation in degenerating plastids or chromatophores such as have been described in flowers [Guilliermond et al. (20)]. The appearance which has been interpreted as a vacuole is

rather the inclusion of a small amount of protoplasm as a result of the amoeboid movements of the plastid at this time.

It is worth emphasizing here that the complete degeneration of the plastids may occur without involving the death of the cell. It has already been noted by Beer (4) that such a phenomenon occurs in some floral organs where the life of the mature cells is comparatively brief. I have found no record, however, of the degeneration of the plastids in cells which remain alive for months thereafter, a phenomenon found in the rhizomes of *Iris macrosiphon*.

In general, it may be stated that there is no sharp line of demarcation between elaioplasts, plastids, chondriocots and mitochondria. In *Iris* they have all been observed to form starch and, with the exception of mitochondria, chlorophyll, oil and a yellow pigment. In some instances several of these products may appear at once, or they may develop in succession, or none of them may form. Nor should any of the chondriocots and plastids be considered end products of a developmental series originating from mitochondria-like bodies, for until irreversible changes occur such as a resolution into structureless spheres of oil, the shapes assumed are reversible. In other words there is no clear distinction between amyloplasts, leucoplasts, chloroplasts, chromoplasts and elaioplasts; nor is it possible to consider plastids, chondriocots, proplastids and mitochondria as unrelated cell structures. Rather it appears that these are all forms of the same fundamental cell organ differing only in size and in the chemical products being formed at the time.

3. SIGNIFICANCE OF THE STUDY OF OIL-BEARING PLASTIDS IN IRIS FROM A TAXONOMIC VIEWPOINT

The occurrence of two types of plastids in rhizomes of *Iris* each more or less restricted to certain groups of species appears to be of taxonomic significance. The consistent appearance of the same type in well defined species indicates a character that may be useful in separating species. In addition it should be noted that the substitution of compound starch grains for the elaioplasts in rhizomes of a known hybrid and in one or two questionable species, although not an invariable phenomenon, suggests a possible means of identifying some plants as of hybrid origin.

CONCLUSIONS

1. The anomalous bodies in the rhizomes of *Iris versicolor* are an elaioplast phase of leucoplasts persisting throughout the resting season, but forming starch throughout the actively growing period.

2. Some, if not all, of the so-called "elaioplasts" are plastids in some form or other.

3. Elaioplasts of the plastid type are not necessarily degeneration types: in *Iris* they are functional plastids.

4. The rotary movement of elaioplasts described in the literature is an artefact due to slow death or injury; the Brownian movement described as characteristic of globules in certain liverworts is a degeneration or injury phenomenon.

5. The elaioplasts in *Lunularia* and *Vanilla* are morphologically similar in that they are aggregations of small plastid-like bodies that form oil. This establishes another link between elaioplasts in the liverworts and those in the monocotyledons.

6. There is no sharp line of demarcation between the different kinds of plastids and chondriosomes each of which is a more or less temporary form capable of changing to the other types.

7. At all times the plastids are more or less plastic but particularly so in young tissues, fibrovascular tissue or slowly dying cells.

8. Leucoplasts, chloroplasts and chromatophores do not go through a set series of changes in developing from plastid types characteristic of meristematic tissues. They may pass through various series depending upon the type of mature tissue involved, or they may merely increase in size with probable changes in their physico-chemical structure. They never form by budding of chondrioconts succeeded by separation of the buds so-formed.

9. Chondrioconts may form an intermediate developmental stage in the formation of "mature" plastids, although not necessarily; they may persist in some tissue; or they may be an intermediate stage in the degeneration of plastids.

10. Plastids and chondriosomes in *Iris* all show the structure of a matrix with embedded globules. Pigments are more soluble in the globules than in the matrix, although they are found in both.

11. Two types of degeneration of plastids occur involving (a) an increasing fluidity and a decreasing refractivity or (b) a complete breaking down into large homogeneous spheres of oil. Degeneration of the plastids does not necessarily involve the death of the cell.

12. The formation of a vacuole with at times an included oil drop in degenerating chondrioconts is in reality an inclusion of protoplasm.

13. Different species of *Iris* are characterized by distinct types of elaioplasts in their rhizomes. The distribution of types follows closely the taxonomic groupings and may be of significance in separating species.

14. The occurrence of such elaioplasts as those in rhizomes of *Iris versicolor* is confined, so far as could be ascertained, to rhizomes of this genus. For the most part they are restricted to rhizomes of certain species, chiefly Apogons of Asia and America.

15. Refractive bosses on pollen grains of *Iris Xyphium* are oil-bearing chromatophores adhering from the tapetal fluid. Other markings found on pollen grains were part of the wall structure.

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DESCRIPTION OF PLATES

Figs. 1-4, 6, 8-10, 38, 39, 45, 46 were made with a camera lucida; the magnifications given for these figures are exact. The other figures were drawn free-hand; the magnifications given for them are approximate.

PLATE 132

- Fig. 1. *Iris versicolor* L. Living cells of the rhizome from material collected in December. $\times 475$.
- Fig. 2. Individual elaioplasts from cells shown in Fig. 1. $\times 1600$.
- Fig. 3. Individual elaioplasts from cells shown in Fig. 1 after treatment with (a) ammonium Erliki fixative, and erythrosin and cyanin; and (b) 0.5% osmic acid. $\times 1600$.

- Fig. 4. *Iris versicolor* L. Individual elaioplasts from rhizomes collected in October: (a) surface view; (b) included starch grains; (c) diagram to illustrate position, size, number and shape of starch grains. $\times 1600$.
- Fig. 5. *Iris versicolor* L. Individual elaioplasts treated with Gram's solution: (a) material from Duxbury, Mass.; (b) material from Lincoln, Mass. These were drawn at the same magnification.
- Fig. 6. Isolated starch grain from elaioplast shown in Fig. 4. $\times 1600$.
- Fig. 7. *Iris tectorum* Maxim. Elaioplasts from young cells of rhizomes collected in March: (a) normal plant; (b) dying plant. $\times 845$.

PLATE 133

- Fig. 8. *Iris pallida* Lam. $\times ?$ Living cell of the rhizome from material collected in December. $\times 475$.
- Fig. 9. Individual oil-bearing plastids from cell shown in Fig. 8 showing plastids: (a) without starch; (b) with starch; (c) is a diagram showing the relative positions of plastid and starch. $\times 1600$.
- Fig. 10. Individual starch grains from plastids similar to those shown in Fig. 9. $\times 1600$.
- Fig. 11. *Iris pumila* L. Oil-bearing plastids from living cells of a rhizome collected at St. Louis in March: (a), (b) and (c) are plastids from successively older cells. $\times 1270$.
- Fig. 12. Oil-bearing plastids from living cells of rhizomes of the following California species of *Iris*: (a) *I. missouriensis* Nutt.; (b) *I. Douglasiana* Herb.; (c) *I. longipetala* Herb.; (d) *I. Hartwegii* Baker. Material collected in California in August. $\times 1270$.
- Fig. 13. Diagram showing the types of oil-bearing plastids found in *Iris* species in March. See table p. 246 for names.

PLATE 134

- Fig. 14. *Iris macrosiphon* Torr. Elaioplasts in living cells from the cortex of a rhizome collected in July: (a), (b) and (c) are taken from successively older cells. $\times 1245$.
- Fig. 15. Elaioplasts shown in (a) Fig. 14b and (b) Fig. 14c treated with Gram's solution to show the surrounding cytoplasm. $\times 1245$.
- Fig. 16. *Iris Xyphium* L. Optical section of living pollen grain. $\times 500$.
- Fig. 17. *Iris Xyphium* L. Untreated pollen grains in surface view: (a) in tapetal fluid of immature anther; (b) from a ripened anther. $\times 475$.

PLATE 135

- Fig. 18. *Iris macrosiphon* Torr. Oil-bearing plastids in living epidermal cells of root-tip: (a), (b), (c) and (d) are from successively older cells. $\times 1280$.
- Fig. 19. *Iris versicolor* L. Elaioplasts from living cells of the meristem of a rhizome: (a) from one of the youngest cells; (b) and (c) from successively older cells. $\times 1620$.
- Fig. 20. *Iris pallida* Lam. $\times ?$ Plastids from living, elongated, differentiating cells of root-tip: (a) successive observations on a single plastid to show fluctuating variations in form; (b), (c), (d) and (e) similar observations on four additional plastids. $\times 1620$.
- Fig. 21. Plastid similar to those in Fig. 20 but from an older cell. $\times 1620$.
- Fig. 22. Plastid similar to that shown in Fig. 21. $\times 1620$.
- Fig. 23. Plastid similar to that shown in Fig. 21. $\times 1620$.
- Fig. 23a. Plastid similar to that shown in Fig. 21. $\times 1620$.



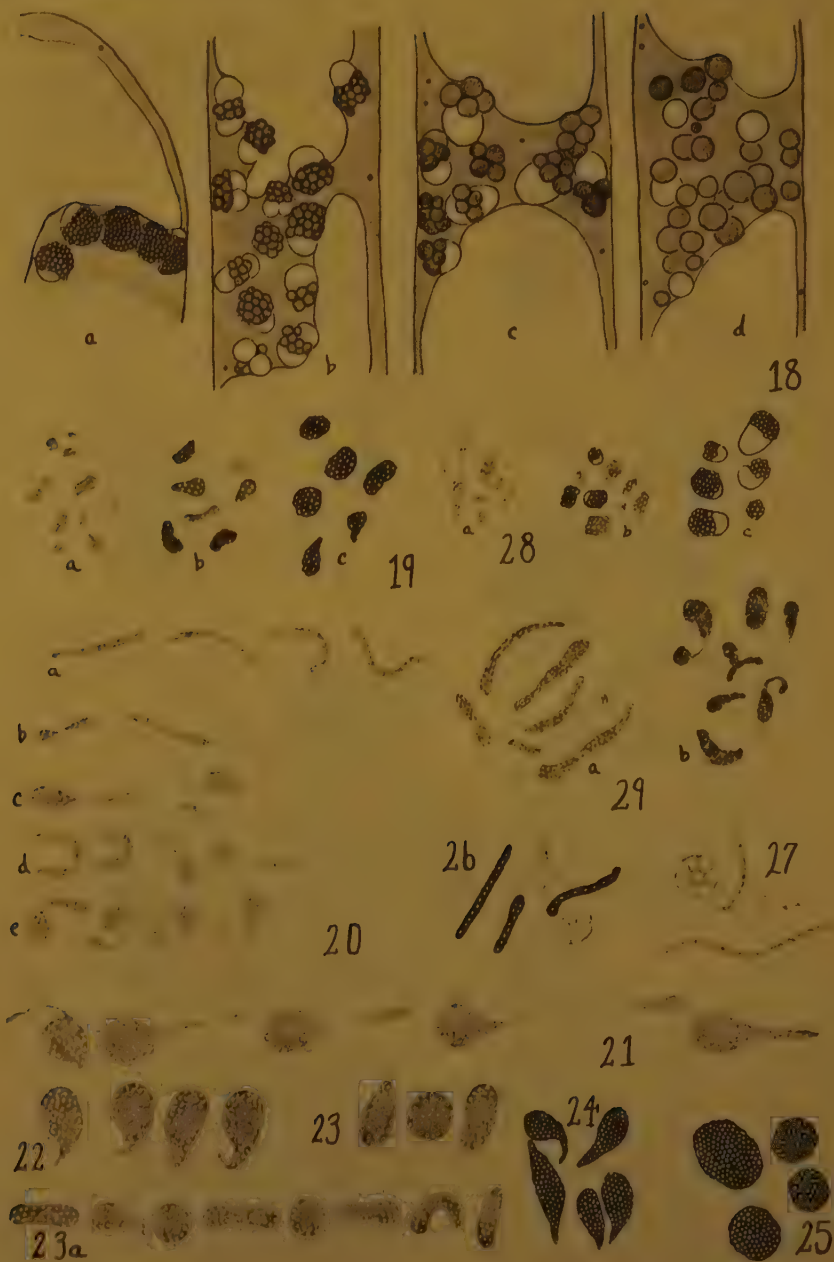
ELAIOPLASTS IN IRIS



ELAIOPLASTS IN IRIS



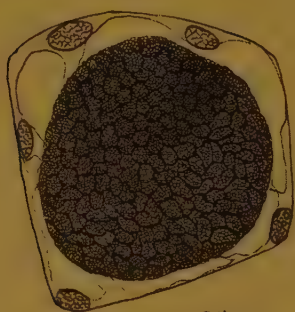
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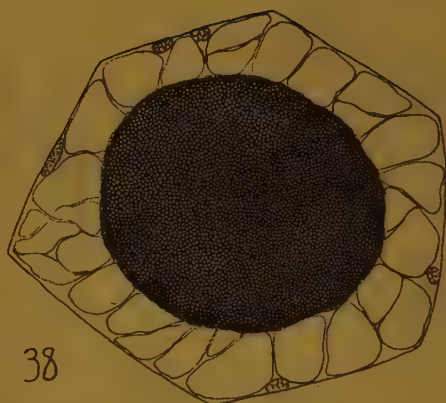
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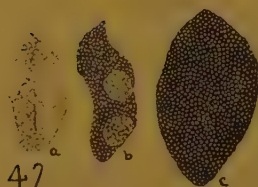
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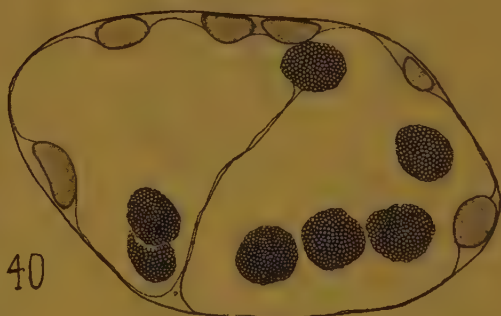
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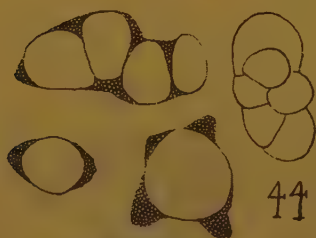
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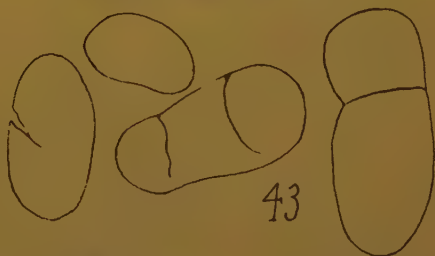
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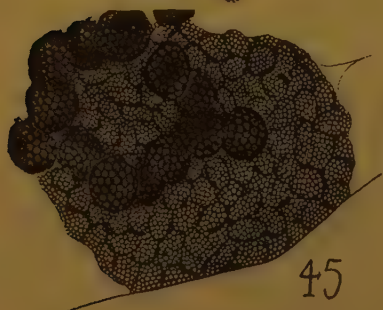
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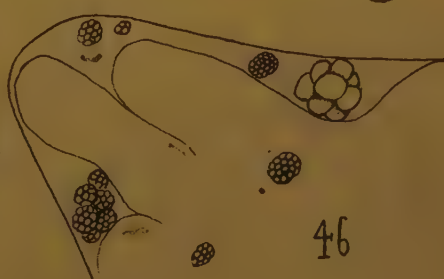
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ELAIOPLASTS IN IRIS

- Fig. 24. *Iris pallida* Lam. \times ? Elaioplasts from living cells of cortex of root-tip. \times 1620.
- Fig. 25. *Iris pallida* Lam. \times ? Elaioplasts from living cells of cortex of older root. \times 1620.
- Fig. 26. *Iris pallida* Lam. \times ? Plastids and chondriosomes from a single living cell of the central cylinder of a root-tip. \times 1620.
- Fig. 27. Plastids and chondriosomes from another cell of the central cylinder. \times 1620.
- Fig. 28. *Iris pallida* Lam. \times ? Oil-bearing plastids from living cells of the meristem of a rhizome: (a), (b) and (c) are from successively older cells and show the appearance of starch. \times 1620.
- Fig. 29. *Iris pallida* Lam. \times ? Chromoplasts from living cells of the root-cap: (a) and (b) are from successively older cells. \times 1620.

PLATE 136

- Fig. 30. *Iris pallida* Lam. \times ? Elaioplasts from living cells of cortex of root-tip. \times 1650.
- Fig. 31. *Iris pallida* Lam. \times ? Chromatophores from living cells of the epidermis of the root-tip: (a), (b), (c) and (d) from successively older cells. \times 1650.
- Fig. 32. *Iris versicolor* L. Plastids from living cells of the epidermis of a root-tip. \times 1650.
- Fig. 33. *Iris pallida* Lam. \times ? Chromatophores from living cells of the epidermis of a root-tip. \times 1650.
- Fig. 34. Chromatophores from living cells of the epidermis of a flower of a Pogoniris, probably of *I. variegata* L. \times 1650.
- Fig. 35. *Iris versicolor* L. Oil-bearing plastids from living cell of cortex of root. \times 1650.
- Fig. 36. *Iris versicolor* L. Chloroplasts from living parenchyma cells of a leaf: (a) without starch; (b) with starch. \times 1650.
- Fig. 37. *Iris versicolor* L. Plastids from living cells of the epidermis of a leaf. \times 1650.

PLATE 137

- Fig. 38. *Lunularia cruciata* (L.) Dum. Living elaioplast-bearing cell from a mature thallus. \times 1080.
- Fig. 39. *Lunularia cruciata* (L.) Dum. Living elaioplast-bearing cell from the younger tissue of a mature thallus. \times 1080.
- Fig. 40. One of the Jungermanniales. Living cell from a mature leaf. \times 1250.
- Fig. 41. Oil bodies from living cells of leaves of three different species of the Jungermanniales. \times 1250.
- Fig. 42. One of the Jungermanniales. Oil bodies from living differentiating cells of stem: (a), (b) and (c) from successively older cells. \times 1250.
- Fig. 43. One of the Jungermanniales. Oil bodies from living cells of mature plant. \times 1250.
- Fig. 44. One of the Jungermanniales. Oil bodies from living cells of younger tissue. \times 1250.
- Fig. 45. *Vanilla Pompona* Schiede. Elaioplast and chloroplasts from living cell of a leaf. \times 915.
- Fig. 46. *Vanilla Pompona* Schiede. Elaioplasts, chloroplast and chondriosomes in living cell of cortex of root-tip. \times 1720.

NOTES ON YUCCA

SUSAN DELANO MCKELVEY

*With plates 138 and 139****Yucca Thornberi*, spec. nov.**

Plate 138

Trunci 0.75–1.75 m. alti, congesti, infra foliis siccis reflexo-patentibus arcte obtecti, supra comam magnam satis elongatam foliorum viridium gerentes. Folia lineari-lanceolata, 0.30–1 m. vel ad 1.20 m. longa, 1.5–3.5 cm. lata, a basi vel a medio paullo latiore apicem versus attenuata, acuminata, pungentia, concava, utrinque laevia, luteo-viridia, stricta vel leviter recurva, flexibilia, initio margine saepe evanescenter denticulata, mox filifera filis crassiusculis curvatis tarde deciduis, parte basali 2.5–7.5 cm. longa et 7–12.5 cm. lata. Inflorescentia scapo 22–45 cm. longo incluso 1–1.30 cm. alta, angusta, basi et apice attenuata, folia quarta parte vel dimidio superantes; ramuli circiter 25, initio erecto-ascendentes, demum patentes; bractee magnae, late triangulares; flores campanulati, 7.5–12.5 cm. longa; pistillum 5.5–7.5 cm. longum, ovario plerumque oblongo rarius attenuato, $4\frac{1}{2}$ ad $6\frac{1}{2}$ longiore quam lato, stylo 5–6 mm. longo, stigmatibus sub anthesi erectis vel fere erectis; filamenta 4–6.5 cm. longa, apice clavato brevi pro parte inferiore longo gracili. Fructus 13–17.5 cm. longus, 3–4.5 cm. diam., baccatus, incrassatus, apicem versus attenuatus et 2.5–5 cm. sub apice subito constrictus parte constricta plus minusve recurvata.

ARIZONA. Pima Co.: foothills of the Rincon Mts., slightly north of Rincon Creek, a tributary of Pantano Wash, elevation 3600 ft., *S. D. McKelvey*, no. 1627, March 23, 1930 (type; herb. Arnold Arboretum). Also from the same region are the author's collections nos. 1585, 2123, 2556, 2557, 2558, 2559, 2561, 2562, 2682, 2684.

Yucca Thornberi forms large and crowded clumps and produces many rather long stems 2–5 ft. in height which are covered below with a thick thatch of reflexed-spreading dead leaves and are crowned by large, somewhat elongated heads of green foliage which are constricted near the base and spreading above; the slightly broadened, concave, not conspicuously angled leaves are commonly smooth on both surfaces, yellow-green in color, with acuminate apex and, when young, often evanescently denticulate margins which, when the foliage is more mature become abundantly filiferous; the fibres are late-deciduous, moderately coarse

and loosely curled. The inflorescence is for some time rather fleshy and brittle, 3-4 ft. in length overall, with a scape 9-18 in. in length; the inflorescence proper is long, narrow, tapered at both ends, and extends for $\frac{1}{4}$ - $\frac{1}{2}$ its length above the leaves; its branchlets are about 25 in number, at first erect-ascending, eventually spreading; its bracts are large, fleshy to leathery, broad-triangular in form. The flowers are campanulate, large, 3-5 in. in length; the pistil is $2\frac{1}{8}$ -3 in. long with a commonly oblong, only rarely tapered, ovary which is $4\frac{1}{2}$ - $6\frac{1}{2}$ times as long as broad, the short style is $\frac{3}{8}$ - $\frac{1}{4}$ in. long and, at anthesis, with erect, or nearly erect stigmas; the filaments vary from approximately $1\frac{1}{2}$ - $2\frac{1}{2}$ in. in length and reach anywhere from slightly below to slightly above the shoulders of the ovary; their clavate tip is short in proportion to the long, slender, lower portion. The baccate fruit is 5-7 in. in length, slightly enlarged and tapered upward for its major lower portion, for 1-2 in. below the tip much contracted and commonly somewhat recurved.

Yucca Thornberi appears to be most closely related to *Y. arizonica* and to *Y. baccata* Torr., differing conspicuously from the latter in habit of growth, from both species it is distinct in form of inflorescence, in character of foliage and, though less so, in fruit.

It is a pleasure to give to this new species the name *Yucca Thornberi* in recognition of the fact that Dr. J. J. Thornber of the University of Arizona called the author's attention to the plant and with her spent considerable time in its study.

***Yucca brevifolia* Engelm. var. *Jaegeriana*, var. nov. Plate 139**

A typo recedit habitu humiliore vix 3-4 m. excedente, trunco brevi circiter 75-90 cm. longo, ramis brevibus fere erectis arcte congestis, foliis circiter 10 cm. longis vel 20 cm. vix excedentibus comam congestam et symmetricam formantibus, inflorescentiis vix 30 cm. longis, scapo 2.5-5 cm. longo et 2.5-3 cm. crasso incluso, ramulis tantum 2.5-6.5 cm. longis.

CALIFORNIA. San Bernardino Co.: vicinity of the Shadow Mts., elevation approximately 4000 ft., *S. D. McKelvey*, no. 2732, April 30, 1932 (type; herb. Arnold Arboretum).

In several of the broad basins and foothill areas of the eastern part of the Mohave Desert of California and also in southern Nevada, occurs a form of the Joshua-tree which deserves varietal recognition. The plant—in appearance a miniature Joshua-tree—was brought to the attention of the writer by Mr. Edmund C. Jaeger of Riverside Junior College, Riverside, California, and is named in appreciation of this fact.

This variety is primarily distinguished from the better known plant by its dwarfer habit,—the plants not exceeding, except rarely and only in extremely old specimens, 10–12 ft. in height; the trunk is short, about $2\frac{1}{2}$ –3 ft. in length, stout (although, proportionately to that of the type of the species, slender); the branches are short, nearly erect and form an extremely dense, compact crown; the clusters of green leaves are crowded and symmetrical, about 1–2 ft. in length; the leaves are short, including the base about 4 in. long, not exceeding 8 in.,—or about the length of the shorter leaves of the type of the species; the inflorescence scarcely reaches 1 ft. in length; the scape is 1–2 in. long, $1\frac{1}{4}$ in. in diameter at base, and the flowering portion 9–10 in. in length with stout branchlets only $1\text{--}2\frac{1}{2}$ in. long. In flower and in fruit characters it is very similar to the plant of taller habit.

Mr. Jaeger states (in litt., Oct. 2, 1934) that the distribution of the variety “reaches its greatest density in the vicinity of the New York Mts. in California.” It has been collected by the writer in southern Nevada between the Colorado River and Searchlight (no. 4094), in the Spring Mts. (no. 4142) and on the eastern slopes of the Charleston Mts. (nos. 4097, 4098, 4099, 4100, 4132), in the first and last of which regions it occurs in abundance.

***Yucca arizonica*, nom. nov.**

Yucca puberula sensu Torrey in Botany, Emory Report, 221 (1859), in part, not Haworth.

Yucca brevifolia Schott ex Torrey, Botany, Emory Report, 221 (1859), in part, as synonym of *Y. puberula* Torrey, not Haworth. — Engelmann in Trans. Acad. St. Louis, 3:46 (1873), in part, as synonym of *Y. Schottii* Engelm. — Trelease in Rep. Mo. Bot. Gard. 13: 100, tt. 57–59, 96 (fig. 2, range map) (1902), first appearance as a valid species. — Not *Y. brevifolia* Engelm. (1871).

Yucca Treleasei MacBride in Contrib. Gray Herb. ser. 3, no. 56: 15 (1918); not *Y. Treleasei* Sprenger (1906).

The name *Y. puberula* Haw. was first erroneously applied by Torrey to specimens collected by Arthur Schott in regions adjacent to Nogales, Arizona. Because of its connotation it is in the main referable to *Y. Schottii* Engelm., the inflorescences of which species are commonly puberulous. Schott's material represented a complex. For a certain portion of this material the name *Y. brevifolia* used by Schott in his notes was adopted by Trelease in 1902. This name, as pointed out by MacBride in 1918 was antedated by the name *Y. brevifolia* used by Engelmann in 1871 for the Joshua-tree; MacBride in consequence gave to Schott's plant the new name *Y. Treleasei*.



YUCCA THORNBERI McKelvey
A plant growing at the type locality.



YUCCA BREVIFOLIA var. *JAEGERIANA* McKelvey
A plant, 12 ft. in height, growing at the type locality.

Unfortunately the name *Y. Treleasei* was used by Carl Sprenger in 1906 for a hybrid *Yucca* (See Bull. Soc. Tosc. Ort. 31: 134. 1906.—Molon, Yucche, 192, t. 6. 1914); the plant is without a name and the new name *Yucca arizonica* is here adopted for this species.

ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

